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THE GENERA OF SPHENOCLEACEAE AND CAMPANULACEAE IN THE SOUTHEASTERN UNITED STATES[1]

THOMAS J. ROSATTI[2]

SPHENOCLEACEAE A. P. de Candolle, Prodr. 7(2): 548. 1839, nom. cons.

(SPHENOCLEA FAMILY)

A monogeneric family of one or two species of annual herbs that inhabit wet places. The plants are distinguished by nonmilky sap; erect, spongy, fistulous,

[1]Prepared for the Generic Flora of the Southeastern United States, a long-term project currently made possible through the support of National Science Foundation Grant BSR-8303100 (Norton G. Miller, principal investigator), under which this account was prepared, and BSR-8111520 (Carroll E. Wood, Jr., principal investigator). The 109th in the series, this paper follows the format established in the first one (Jour. Arnold Arb. **39:** 296–346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets [ ]. The references that I have not verified are marked with asterisks.

I thank Norton Miller and Carroll Wood for the opportunities provided by the Generic Flora project; for their open-mindedness and absolute standards of excellence; and for their help throughout this investigation. I am also grateful to George K. Rogers and Ihsan A. Al-Shehbaz for their generous assistance, particularly during my visits to Harvard; to Warren H. Wagner, Jr., always an important source of information; to Nancy R. Morin, who contributed valuable intelligence about *Campanula*; to Michael A. Canoso and Jimmy R. Massey for special efforts to provide specimens for my examination; and to Elizabeth B. Schmidt and Stephen A. Spongberg, who carefully reviewed the final manuscript. Collections from the libraries and/or herbaria associated with the New York State Museum, Harvard University, the New York Botanical Garden, the University of Michigan, Michigan State University, and the University of North Carolina were utilized in this study, and thanks are due the respective librarians and/or curators of these institutions.

Figure 1 (*Triodanis*) was prepared by Rachel A. Wheeler under the supervision of George K. Brizicky, from preserved material collected by Carroll Wood and Alan Strahler near Fort Meade, Florida (*CEW 9020*). Figure 2 (*Lobelia*) was drawn by Virginia Savage with the guidance of Carroll Wood (who also prepared the dissections), from plants cultivated by Alice F. Tryon in Lexington, Massachusetts (a, b, k, l, m) and from preserved flowers of plants grown by the late Richard J. Eaton in Lincoln, Massachusetts (c–j).

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somewhat succulent stems; simple, alternate, exstipulate, petiolate, entire leaves; terminal, densely spicate (the axes completely hidden), clearly acropetal, pedunculate inflorescences; perfect, actinomorphic, sessile flowers, each subtended by a bract and two bracteoles; green calyces with deltoid to suborbicular, imbricate lobes that encase both flower buds and fruits (and thereby render most of the inflorescence/infructescence green); white to pale yellow, caducous corollas with imbricate lobes; short filaments and rounded anthers; mostly inferior, bilocular ovaries with numerous ovules and large, spongy, axile placentae; and membranaceous, circumscissile, bilocular, many-seeded capsules. TYPE GENUS: *Sphenoclea* Gaertner.

1. **Sphenoclea** Gaertner, Fruct. Sem. Pl. **1:** 113. 1788, nom. cons.[3]

Erect, glabrous annuals (reportedly sometimes perennials) of moist to wet places. Stems without milky sap, freely branched, somewhat succulent, hollow. Leaves ovate to elliptic; base cuneate, sometimes slightly oblique; apex acute to rounded, sometimes mucronate; venation pinnate and somewhat arcuate. Inflorescences terminating the main stem or axillary branches, acropetal, densely spicate, pedunculate. Flowers perfect, laterally compressed, sessile, attached by a narrowly elliptic, longitudinally oriented base and each subtended by a single, spatulate, acute to acuminate, green-tipped bract and 2 slightly smaller, more nearly linear, green-tipped bracteoles. Calyx synsepalous below, actinomorphic; lobes 5, deltoid to suborbicular, slightly erose, curved inward, imbricate, persistent and enlarging in fruit. Corolla sympetalous below, actinomorphic; lobes 5, alternate with the calyx lobes, rounded, slightly erose, curved inward, imbricate, exceeding the calyx at anthesis, caducous. Stamens 5, not connate, adnate to the corolla and alternate with its lobes; filament short; anther rounded, 2-locular at anthesis, longitudinally dehiscent. Ovary mostly inferior, 2-locular; placentae spongy, stipitate, axile; style short or not apparent, collecting hairs absent; stigma capitate, slightly bilobed, sessile or nearly so. Ovules numerous, anatropous, unitegmic, tenuinucellate. Fruit a cuneate-obconical, 2-locular, membranaceous, circumscissile capsule, mostly encased in the persistent calyx lobes. Seeds numerous, small, oblong, yellowish brown, lustrous, longitudinally striate with indistinct pits between the ridges; endosperm cellular; embryo straight, filling the seed, its development of the Onagrad type. (*Pongati* Adanson, nom. illeg.; *Pongatium* Juss., nom. illeg.) TYPE SPECIES: *S. zeylanica* Gaertner. (Name probably from Greek *sphēn,* a wedge, most likely in reference to the capsule, which is wedge shaped below by compression; Gaertner's original description of *Sphenoclea* included the phrase "capsula infera, cuneiformi-compressa, bilocularis, circumscissa.")

A small genus composed of one or two species of herbs. *Sphenoclea zeylanica* Gaertner, $2n = 24$, and the West African endemic *S. Pongatium* DC. have been recognized, but the latter is commonly lumped under *S. zeylanica,* and almost all of the literature deals with plants to which this name has been applied.

[3]Conservation superfluous; see Rickett & Stafleu, Taxon **9:** 122. 1960. *Pongatai* Adanson (1757) is not validly published, and *Pongatium* Juss. (1789) is a later synonym.

Sphenoclea differs most conspicuously from members of the Campanulaceae in its densely spicate inflorescences. In habit the genus is often said to resemble *Phytolacca* (Phytolaccaceae). Because of this vegetative similarity and several unspecified anatomical features, Airy Shaw suggested that *Sphenoclea* is taxonomically allied with *Phytolacca* and unrelated to the Campanulaceae. However, although Kovanda proposed a connection between *Sphenoclea* and the Lythraceae, such a position is at odds with the overwhelming majority of botanical opinion.

On the bases of anatomy and morphology of flowers, fruits, seeds, and seedlings, Monod considered the Sphenocleaceae and the Campanulaceae to be related, although Gupta concluded that differences in floral vasculature between *Sphenoclea, Campanula,* and *Lobelia* were not important enough to warrant a separate family for *Sphenoclea.* Maheshwari summarized both anatomical and embryological evidence, including that provided by Subramanyam (1950), and concluded that *Sphenoclea* is related neither to the Phytolaccaceae nor to the Primulaceae (a relationship that Airy Shaw had also considered). In contrast to the Phytolaccaceae, both *Sphenoclea* and members of the Campanulaceae lack anomalous secondary growth and have anatropous, unitegmic, tenuinucellate (vs. anacampylotropous, bitegmic, crassinucellate) ovules and cellular (vs. free-nuclear) endosperm with well-developed haustoria (vs. no haustoria). Hutchinson (1973) and Corner also pointed out some essential differences between *Sphenoclea* and *Phytolacca,* and Cronquist noted that *Sphenoclea* is embryologically and palynologically similar to the Campanulaceae.

Although most botanists have favored an alliance with the Campanulaceae, opinions have varied regarding the taxonomic level at which *Sphenoclea* should be recognized. De Candolle and Boissier each placed the Sphenocleaceae near the Campanulaceae, and both Wagenitz and Cronquist recognized it as one of a number of families in the Campanulales. Corner, Dunbar (1975b), Monod, and Subramanyam (1950), among others, have recognized the genus as a monotypic family related to the Campanulaceae. Baillon's treatment of the Campanulaceae included tribes Sphenocleeae, Campanuleae, and Lobelieae, and Schönland recognized subfamilies Campanuloideae (including tribe Sphenocleeae), Cyphioideae, and Lobelioideae. Bentham & Hooker placed the Campanuleae (including *Sphenoclea*), Lobelieae, and Cyphieae in their Campanulaceae. Dahlgren, Fedorov, Takhtajan, Thorne (1976), and Wilbur are among the modern systematists who have included *Sphenoclea* in the Campanulaceae (see also Moeliono & Tuyn).

Chemical data regarding the affinities of *Sphenoclea* appear to be contradictory. According to Gibbs, raphides (used by Gibbs to mean crystals of calcium oxalate) are present in *Phytolacca* and some related genera but are probably absent from *Sphenoclea* and members of the Campanulaceae. Cronquist (1981), however, indicated the presence of calcium oxalate crystals in the Phytolaccaceae (said to be often raphides), as well as in *Sphenoclea* (whether they are raphides was not indicated).

Treatment of *Sphenoclea* as a separate family seems at this time to be largely a matter of opinion. The decision to do so here is at least in part intended to

accentuate differences that are especially apparent among plants of the southeastern United States. The Campanuloideae and Lobelioideae (and the intermediate and extraregional Cyphioideae) appear to be much more closely related to each other than to *Sphenoclea*. The only other family in the Southeast to have been allied with the Sphenocleaceae and the Campanulaceae is the Goodeniaceae. Although these three families were united by Cronquist at the ordinal level, most recent evidence suggests that the affinities of the Goodeniaceae lie elsewhere (see discussion under Campanulaceae). With the removal of the Goodeniaceae (and the related Brunoniaceae), recognition of the Sphenocleaceae within a more homogeneous and narrowly defined Campanulales seems even more justified.

In addition to having a densely spicate inflorescence, *Sphenoclea* differs from genera of the Campanulaceae in the absence of a specialized mechanism of pollen presentation, as well as in the lack of typical laticiferous phloem canals (although granules in some phloem cells may represent dried latex; see, however, Airy Shaw). Furthermore, *Sphenoclea* has circumscissile capsules, tetracytic instead of mostly anomocytic stomata (see Shah & Mathew), pericyclic stem sclerenchyma, and cluster crystals, instead of fine, mostly acicular ones (Metcalfe & Chalk, 1950).

Sphenoclea zeylanica, $2n = 24$, sheds trinucleate pollen (Kausik & Subramanyam) that is subprolate, tricolporate, and reticulate (Cronquist). Dunbar (1975b) stated that the exine sculpturing (smooth but with round protrusions of varying size) has no relationship with the condition seen in the Campanulaceae.

Reportedly rare in South Carolina (Radford *et al.*) and evidently absent from tropical Florida (see Long & Lakela), *Sphenoclea zeylanica* occurs in moist soil or shallow water throughout most of the remainder of the Coastal Plain in the southeastern United States; it has also been reported from Texas (Correll & Johnston). The species is a native of the Old World tropics and is now widely established in warm areas of the Western Hemisphere. It was collected in Louisiana as early as 1898. Although almost exclusively indicated to be an annual, Radford and colleagues reported it as a perennial.

Sphenoclea zeylanica commonly grows as a weed in rice fields throughout the world. An exudate from the roots of living plants has been shown to serve as an effective and expedient control of the rice-root nematode, *Hirschmanniella oryzae* (Mohandas *et al.*). The pleasant-tasting leaves are eaten with rice by the Javanese (Uphof).

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CAMPANULACEAE A. L. de Jussieu, Gen. Pl. 163. 1789, nom. cons.

(BELLFLOWER FAMILY)

Erect, ascending, decumbent, sometimes prostrate [or caespitose], terrestrial to aquatic, laticiferous, annual, biennial, or perennial herbs (sometimes woody toward the base) [or shrubs or trees to 10 m tall]. Stems simple to much branched, often more so near the base, sometimes rhizomatous [or stems succulent]. Leaves simple, alternate, sometimes opposite or whorled (in 3's), exstipulate, sessile to petiolate, the margins entire, ciliate, undulate, serrate, crenate, or dentate, sometimes lobed. Inflorescences racemose (including globose, involucrate umbels, spikes, or panicles) or cymose, the flowers rarely solitary; floral bracts inconspicuous or leaflike. Flowers perfect [rarely carpellate or staminate, the plants then dioecious], sometimes cleistogamous (and then often with rudimentary or missing parts), sometimes bracteolate, resupinate in the Lobelioideae, proterandrous. Hypanthium sometimes extending shortly above the ovary, sometimes ribbed. Calyx synsepalous, mostly actinomorphic, often with a reflexed appendage in the sinuses between lobes, persistent in fruit; lobes 5 (3, 4, or 6), imbricate or valvate, often linear, frequently longer than the tube, opposite the axis of the inflorescence in the Campanuloideae, alternate in the Lobelioideae (but made opposite by resupination). Corolla sympetalous; lobes 5, alternate with the lobes of the calyx, either actinomorphic and campanulate to rotate (Campanuloideae) or zygomorphic and 2-lipped (Lobelioideae), with the 3 upper petals forming a lower 3-lobed lip and the other 2 forming an upper lip (after resupination) that is 2-lobed and sometimes cleft between the lobes [sometimes to the base of the corolla] [or sometimes all 5 petals more equally connate and less zygomorphic]. Stamens equal in number

to and alternate with the corolla lobes; filaments free from the corolla (and inserted on a disclike nectary) or inserted at its base, free below (connate above in the Lobelioideae); anthers bilocular, with introrse, longitudinal dehiscence, coherent and becoming free after anthesis in the Campanuloideae but connate in the Lobelioideae, in both subfamilies forming a tube into which pollen is released. Pollen 2–12-aperturate; in the Campanuloideae usually porate (rarely colporate) [or colpate] and spinulose; in the Lobelioideae colpate [or colporate] and reticulate. Gynoecium 2–5-carpellate (usually 3 in the Campanuloideae and 2 in the Lobelioideae), carpels fused into an inferior (or sometimes half-inferior) [rarely superior] ovary commonly bearing an annular nectariferous disc and usually with as many locules as carpels or sometimes more by the intrusion of false septa (Campanuloideae) or fewer by the disappearance of septa (Lobelioideae). Style with apical hairs that remove pollen from the anther tube as the base of the style elongates; stigma lobes 2–5, spreading apart after exceeding the anther tube. Ovules numerous on axile (sometimes parietal) placentae, anatropous, tenuinucellar, and with a single, massive integument; megagametophyte of the Polygonum type. Fruit a loculicidal capsule dehiscent by pores or slits either apically (i.e., within the persistent calyx lobes) or laterally [rarely indehiscent or a berry]. Seeds numerous, small; endosperm cellular, oily [rarely starchy]; haustoria at micropylar and chalazal ends; embryo usually straight, not filling the seed, its development of the Solanad type. (Including Lobeliaceae R. Br. Trans. Linn. Soc. London **12:** 133. 1817, nom. cons.) TYPE GENUS: *Lobelia* L.

The family is here considered to include the subfamilies Campanuloideae and Lobelioideae Schönl., as well as the intermediate and extraregional Cyphioideae Schönl. As such, it consists of perhaps as many as 70 genera and 2000 species. The Campanulaceae are of cosmopolitan distribution, although they are best represented in temperate and subtropical regions; tropical species are mostly confined to high elevations. These plants rarely (if ever) grow in pure stands or otherwise occur as dominant vegetational components. Nevertheless, they are often conspicuous because of either showy flowers or unusual habit.

The Campanulaceae are distinguished most readily by a combination of characters including milky sap; rotate, campanulate, or bilabiate corollas; a specialized mechanism of pollen presentation (a stylar brush carries pollen out of and above a variously configured anther tube); and mostly inferior (but sometimes half-inferior or superior) ovaries with axile (rarely parietal) placentae and numerous ovules per locule. Although the varied inflorescences of the Campanulaceae are for the most part very different from the pseudanthium of the Compositae (Asteraceae) (a family that, except for its basal placenta and single ovule per locule, conforms to the foregoing criteria), the globose, involucrate umbel of *Jasione* approaches this design.

The Campanulaceae were placed by Cronquist in his Campanulales with the Brunoniaceae, Donatiaceae, Goodeniaceae, Pentaphragmataceae, Sphenocleaceae, and Stylidiaceae; the Campanulales of Takhtajan and of Thorne were similar to Cronquist's in content, except that Thorne excluded the Stylidiaceae

(including *Donatia* J. R. & G. Forster). Two noncampanulaceous members of the order are represented in the Southeast. *Scaevola Plumieri* (L.) Vahl (Goodeniaceae) is native to southern Florida and other tropical and subtropical areas outside of the Southeast (see Brizicky), and *Sphenoclea zeylanica* Gaertner (Sphenocleaceae) is a species of the Old World tropics that is widely naturalized in warm regions of the Western Hemisphere, including most of the Coastal Plain of North America (see preceding treatment). Carolin (1978) summarized arguments for a saxifragalean origin of the Campanulales (Thorne placed his Stylidiaceae near the Saxifragaceae), while Cronquist favored consideration of the Solanales or their close relatives.

Several botanists have suggested a relationship between the Campanulaceae and the Goodeniaceae, primarily because of similarities in embryology and in the mechanism of pollen presentation. However, the embryological similarities are based on some rather widely distributed character states, and the families differ in certain other embryological features (Vijayaraghavan & Malik). The stylar structures involved in pollen collection (a cup, or indusium, in the Goodeniaceae; hairs in the Campanulaceae) were thought by Carolin (1960) and Cronquist to be analogous. Furthermore, Carolin (1978) has argued that the inferior ovaries of the two groups are not homologous. In his opinion, in the Campanulaceae (where some genera have an extension of the floral tube above the ovary), epigyny resulted from the fusion of a preformed tube of sepals, petals, and stamens to the ovary, while in the Goodeniaceae (where there is no extension above the ovary and, in some genera, a progressive departure of sepals, petals, and stamens from the tube), epigyny resulted from the centrifugal adnation of these parts.

The Goodeniaceae also differ from the Campanulaceae in their more complex cambial anatomy; in the absence of a latex system; in the presence of sclerenchymatous idioblasts (in leaf mesophyll, sometimes in stem cortex as well) and glandular trichomes (Metcalfe & Chalk, 1950; but some species of *Lobelia* have glandular trichomes on the calyx lobes); in their lack of nectaries (but see Carolin, 1959) and of haustoria in the endosperm (Vijayaraghavan & Malik); in the absence of cystoliths (Cronquist); in their pollen (see below); in their complete lack of ellagic acid and tannins (Cronquist); and in the presence of iridoids (Dahlgren *et al.*, Jensen *et al.*). Jensen and colleagues discovered secoiridoids in two genera of Goodeniaceae (including *Scaevola*) and therefore concluded that the group should be recognized as an order distinct from the Campanulales and more closely related to the Gentianales, Dipsacales, and/or Cornales. Vijayaraghavan & Malik also favored a unifamilial Goodeniales, primarily on embryological grounds, but considered it very close to the Campanulales.

Some authors have proposed an origin of the Goodeniaceae within the Lobelioideae. However, although both groups have zygomorphic corollas with slits, the slit in the sympetalous corolla is made adaxial by resupination in the Lobelioideae, while in the Goodeniaceae it is adaxial and there is no resupination. Furthermore, the two-locular ovary of these groups is characteristic of a number of diverse families, and it has been interpreted by Carolin (1960), primarily on the basis of vascularization, to have been derived from two carpels

in the Lobelioideae and from four (accompanied by the loss of two septa) in the Goodeniaceae.

Carolin (1978) concluded that while the Campanulaceae are the nearest relatives of the Goodeniaceae, the relationship is not a close one. He considered the two groups to have evolved (presumably from a common ancestor) in Gondwanaland, the Campanulaceae in the west and the Goodeniaceae in the east. Takhtajan considered the Goodeniaceae (including the Brunoniaceae as a subfamily) to be less related to the remainder of the Campanulales and recognized the suborder Goodeniineae within that order.

The Campanulaceae are among a number of families that have traditionally been suggested to be ancestral to the Compositae (reviewed by Philipson, 1953). Many early botanists favored such a relationship on the basis of floral morphology, particularly the specialized mechanisms of pollen presentation in the two groups. However, similar specializations occur in several putatively unrelated families within the Asteridae and are therefore thought not to be reliable indicators of relationships (Cronquist). Internal phloem, laticifers, and inulin occur in both the Campanulaceae and the Compositae but are sporadic in other families as well. In nodal anatomy the Compositae (and Goodeniaceae) are trilacunar (or rarely multilacunar), whereas the Campanulaceae are always unilacunar, a condition generally thought to represent an evolutionary reduction from more complex types.

In attempts to determine the origin of the Compositae, consideration of the inflorescence has pointed to both the Campanulaceae and the Dipsacaceae. Although the precise nature of the capitulum in the Compositae is not clear, it has often been compared to what is usually considered to be a cymose head in the Dipsacaceae. The plasticity of the inflorescence in the Campanulaceae is well known, and although both cymose and racemose (as well as intermediate) types occur in the family, the latter is more characteristic and is thought to represent the condition seen in *Jasione* (see Carolin, 1967), a genus of Campanulaceae with involucrate umbels. Nevertheless, although the pedicels of both the Compositae and *Jasione* lack bracteoles, such structures are present in the dipsacaceous inflorescence (Philipson, 1948). In addition, the involucral bracts of the Compositae lack meristematic tissue in their axils. Although the bracts of the Dipsacaceae subtend flowers, the bract axils of *Jasione* are often sterile by floral abortion. Philipson (1948) therefore thought that the capitulum of the Compositae could have been derived by further suppression of the aborted involucral flower in an inflorescence such as that of *Jasione*.

Cronquist pointed out that the Campanulaceae and the Compositae are very similar in the possession of inulin and polyacetylenes, which he considered effective against predators and therefore largely responsible for the evolutionary success of these families. He also stated, however, that the immediate ancestors of the Compositae were shrubs or small trees with opposite leaves and cymose inflorescences, thereby ruling out both the Campanulaceae (herbs, alternate leaves, mostly racemose inflorescences) and the Dipsacaceae (herbs, apical placentae).

Two of the three subfamilies of the Campanulaceae contain over 95 percent of the species; both are represented in the southeastern United States. The

Campanuloideae are readily distinguished from the Lobelioideae by their nonresupinate (vs. resupinate) flowers in which the odd petal is morphologically farthest from the axis of the inflorescence (vs. morphologically nearest but made farthest by resupination); their mostly actinomorphic (vs. zygomorphic), nonfenestrate (vs. often fenestrate) corollas; their free (vs. often connate) filaments; their coherent and eventually free (vs. connate) anthers; and their mostly three (vs. two) carpels united into an ovary with as many or (by the intrusion of false septa) more (vs. one or two) locules. The Campanuloideae (primarily herbs, rarely shrubs) consist of about 35 genera and 600 species, nearly all of which are native to the North Temperate Zone. The group is poorly represented in the Southern Hemisphere, although several small genera are endemic to South Africa, and species of (for example) *Wahlenbergia* occur in Australia, New Zealand, and South America. Conversely, the Lobelioideae (small herbs to trees) comprise about 30 genera and perhaps as many as 1200 species, approximately half of which are indigenous to South America (McVaugh, 1949b). The subfamily is otherwise worldwide in distribution, with 15 genera and many species (particularly of *Lobelia*) occurring in North America (McVaugh, 1943). The subfamily Cyphioideae (about four genera and 70 species in South Africa) is considered to be a link between the two other subfamilies in that its members usually have actinomorphic flowers, apically connate staminal filaments, and free anthers.

Genera of the Campanuloideae represented in the Southeast were placed by Schönland in three subtribes within the tribe Campanuleae. Accordingly, the Campanulinae (sepals opposite carpels, at least when equal in number to them; capsules laterally dehiscent in our species [or otherwise sometimes indehiscent, or even berries]) are represented in our area by *Campanula* and *Triodanis*; the Wahlenbergiinae Schönl. (sepals opposite carpels, at least when equal in number to them, capsules apically dehiscent in our species [or sometimes a berry]) by *Wahlenbergia* and *Jasione*; and the Platycodinae Schönl. (sepals alternate with carpels, capsules apically dehiscent in our species [sometimes laterally in others]) by *Platycodon.*[4,5]

[4]The tribes Pentaphragmeae Schönl. and Sphenocleeae Schönl. comprise the remainder of the Campanuloideae in Schönland's system. Since these are considered here to be separate families, the subtribes of Schönland would more appropriately be elevated to the rank of tribe. Therefore, Endlicher's recognition (in *Genera Plantarum*) of the Campanuleae and the Wahlenbergieae (which included *Platycodon*) is adopted here.

[5]*Platycodon* A. DC., a monotypic genus, differs from *Campanula,* in which it was placed initially, in its large flowers, broadly campanulate corollas, and apical, instead of lateral, capsule dehiscence. In contrast to *Wahlenbergia,* in which it has also been placed (and to *Campanula, Jasione,* and *Triodanis* as well), *Platycodon* has carpels never opposite the calyx lobes (see, however, Ohwi). The most distinctive feature of the genus is the inflated appearance of the corolla before the separation of its lobes.

Platycodon grandiflorus (Jacq.) A. DC., $2n = 16, 18, 28$ (Gadella, 1966a, counted only $2n = 18$ in many plants, considered $2n = 28$ to be erroneous, and did not mention $2n = 16$), is a native of northeastern Asia that has been reported as a waif in Warren Co., North Carolina (Radford *et al.*; I have seen one specimen from this locality). Although several species of *Platycodon* have been described, there is general agreement that these represent forms resulting from human manipulation of *P. grandiflorus.* The species is in great demand for both ornamental and medicinal purposes and has therefore been widely distributed. According to Bailey and colleagues, the plants are hardy in the

The delimitation of genera in the Campanuloideae, and in particular within the Campanulinae (here Campanuleae), is often exceedingly difficult (Gadella, 1966a; McVaugh, 1945b). Many small genera have been segregated from *Campanula,* which despite its progressively narrower circumscription remains of doubtful homogeneity. There is, however, little reason for confusion of genera when only plants in the southeastern United States are considered.

Schönland's treatment of the Lobelioideae involved no structuring between the levels of subfamily and genus, whereas that of Wimmer included two tribes and a number of subtribes. Although both the Delisseeae Reichenb. (top of the ovary flat, fruit indehiscent) and the Lobelieae (top of the ovary conical, fruit dehiscent) are represented in North America, tribes were not used by McVaugh (1943) in his treatment of the species occurring there. (For evidence that the tribes proposed by Wimmer do not merit recognition, see discussion of *Lobelia.*) Our species belong to the genus *Lobelia.*[6]

With the exception of the Cyphioideae, the Campanulaceae have become relatively well known chemically over the past 20 years. Carbohydrates are stored as the fructose- (and probably glucose-) containing polysaccharide inulin (also present in the Goodeniaceae [Cronquist]). Although such compounds are usually of limited taxonomic value, inulin was indicated by Gibbs as most likely to be universal in only two families, the Compositae (Asteraceae) and the Campanulaceae. Acetylenes have been detected in 18 dicot families (Bohlmann *et al.*). Although best represented in the Compositae, they are rather common in the Campanulaceae (e.g., *Campanula* [*C. persicifolia* L., *C. rapunculoides* L.], *Wahlenbergia* [*W. gracilis* (Forster) A. DC.], *Jasione, Platycodon* [*P. grandiflorus*], *Lobelia* [*L. cardinalis* L.]); they have not been reported in either the Sphenocleaceae or the Goodeniaceae. Whereas the acetylenes in the Campanulaceae are aliphatic, those in the Compositae are often aromatic. One group, the tetrahydropyranes, is evidently restricted to (and widespread in) the Campanulaceae (Bohlmann *et al.*).

The chemistry of the latex universally present in the Campanulaceae evidently differs in the two major subfamilies. Although in the Campanuloideae the latex contains polysterols and a phenolic glycoside (campanulin), its chemistry is otherwise poorly known in this group; alkaloids or other toxic substances have not been found in the Campanuloideae (Hegnauer *in* Moeliono & Tuyn). In contrast, subfam. Lobelioideae includes many species that are toxic because

North (presumably the northern United States and adjacent parts of Canada) and are adapted to sunny conditions and loamy soils. Although a number of cultivars are grown in North America, it is unclear whether *P. grandiflorus* has become naturalized anywhere on the continent.

Platyconin, an unusually stable anthocyanin based on delphinidin, has been isolated from the fresh petals of several cultivars and found not to vary among them (Saito *et al.*). *Platycodon* appears to be the only genus in the Campanulaceae that is saponiferous (Agarwal & Rastogi).

[6]According to McVaugh (1940a, 1943) the lobelioid and monotypic *Hippobroma* G. Don (included by Wimmer in *Laurentia* Adanson) is represented in the Southeast (Gulf Coast from Florida to Central America) by *H. longiflora* (L.) G. Don (*Lobelia longiflora* L.), a widely established escape from cultivation perhaps originally native to the West Indies. However, Ward contended that collections indisputably from Florida were unknown and that (as of 1978) the species did not occur in the state. According to Ward, its leaves and latex are extremely poisonous.

of alkaloids that are restricted to the latex (about 30 structurally related alkaloids have been found in *Lobelia inflata* L.). Pyridine alkaloids are present in the Lobelioideae (and in particular in a number of Southeastern species of *Lobelia*) and also in the Compositae (see primarily Hegnauer, 1954).

Ramstad was evidently the first to report phenolic compounds in the Campanulaceae. He tested over 1000 species of angiosperms in 238 genera and nine families (not including either the Sphenocleaceae or members of the Campanuloideae) for chelidonic acid and found that of 15 genera of Lobelioideae examined, eight (including ten Southeastern species of *Lobelia*) contained the compound. Bate-Smith surveyed a very large number of taxa for phenolics and found that they were more common in the Campanuloideae than in the Lobelioideae. Caffeic acid (e.g., in *Campanula*) and *p*-coumaric acid (e.g., in *Campanula* and *Jasione*), perhaps the most common phenolic compounds among angiosperms (Gibbs), have frequently been identified in members of the Campanuloideae but are apparently absent in the Lobelioideae. Quercetin and kaempferol were found in *Campanula*; ferulic acid in genera including *Campanula, Jasione,* and *Lobelia*; cyanidin in *Centropogon* (Lobelioideae); and sinaptic acid in *Lobelia*. Both the Compositae and the Campanulaceae are among the several families that generally lack both leucoanthocyanins and the trihydroxy constituents leucodelphinidin, myricetin, and ellagic acid.

Flavonoids in general are not especially well represented in the Campanulaceae. However, anthocyanins have been found in *Campanula* (a pelargonidin [Asen *et al.*]), in *Platycodon grandiflorus* (platyconin [Saito *et al.*]), and in *Lobelia* (a delphinidin that is possibly unique among flavonoids [Yoshitama]); campanoside, cynaroside, and luteolin have been reported in *Campanula* (Teslov, 1977a, 1977b; Teslov & Teslov; Teslov & Zapesochnaya); and luteolin has been identified in *Jasione montana* L. (Zapesochnaya *et al.*).

Cyanogenesis appears to be rare in the Campanulaceae. Gibbs reported negative results for 28 species (e.g., in *Campanula* [including *C. rapunculoides*], *Wahlenbergia, Jasione, Platycodon* [*P. grandiflorus*], and *Lobelia* [including *L. cardinalis, L. inflata*]). Tjon Sie Fat obtained consistently negative results for species including *Campanula persicifolia, C. rapunculoides,* and *Jasione montana* but detected triglochinin in several species of *Campanula,* including the extraregional and polymorphic *C. rotundifolia* L. In this species cyanogenesis is variable. Although more than half of the plants tested released HCN, others lacked either triglochinin or the enzyme necessary for its hydrolysis. The presence in the Campanulaceae of triglochinin, a tyrosine-derived cyanogenic glucoside, is notable in that such compounds in the Compositae are either valine- or phenylalanine-derived (Tjon Sie Fat; see also Saupe).

The Campanulaceae are not saponiferous (see Seigler), with the exception of *Platycodon grandiflorus* (see Agarwal & Rastogi); and they lack iridoid compounds (Gibbs; see also Jensen *et al.*). Although Bate-Smith and Metcalfe & Chalk included the Campanulaceae among families in which all species lacked tannins, Gibbs reported tannins from at least six genera of Campanuloideae and one of Lobelioideae (genera not indicated; see Moreira).

A great deal of cytological diversity exists within the Campanulaceae. Basic chromosome numbers range from $x = 5$ (probable) to $x = 17$, possibly due to

a period of fluctuation early in the history of the group (Contandriopoulos). Some genera (including *Campanula*) are extremely complex cytotaxonomically, with several base chromosome numbers, while others (including *Wahlenbergia, Jasione, Platycodon,* and *Lobelia*) appear to be monobasic.

According to Brewbaker, trinucleate pollen occurs widely in members of both major subfamilies and in *Sphenoclea* but is unknown in other members of the Campanulales (pollen of the Goodeniaceae is binucleate). Binucleate pollen occurs in genera including *Campanula, Jasione,* and *Platycodon,* while *Lobelia* is one of ten genera of flowering plants in which both bi- and trinucleate pollen are present (pollen of *L. cardinalis* is binucleate). Davis reported that the pollen is two celled when shed in *Campanula americana* L. and in an extraregional species of *Wahlenbergia,* but three celled in *W. gracilis.*

Pollen morphology in the Campanulaceae and related families was studied by Dunbar (1973a, 1973b, 1975a, 1975b). The exine is usually spinulose in the Campanuloideae and reticulate in the Lobelioideae, but there are exceptions. Both conditions occur in species of the extraregional campanuloid genus *Phyteuma* (Dunbar, 1973a, 1975a). In genera including *Campanula, Wahlenbergia,* and *Platycodon* the spinules are often divided at the base. The pollen in the family has from two to 12 apertures of various kinds that at least in *Campanula* and *Jasione* may be operculate as well. The apertures in the Campanuloideae are porate in most genera (e.g., *Campanula, Triodanis, Wahlenbergia, Jasione*), colporate in some (e.g., *Platycodon*), and colpate in others. Aperture type in this subfamily does not agree well with the subtribes of Schönland but is correlated with pollen shape. Porate, colporate, and colpate grains occur in the Campanulinae and Wahlenbergiinae, and both porate and colporate types are found in the Platycodinae (see also Erdtman). Porate grains are spherical to oblate-spherical, while colpate and colporate pollen is frequently prolate, increasing in equatorial width (i.e., becoming more oblate) with increasing numbers of apertures. Porate grains in the Campanuloideae are considered to have developed in connection with a migration to the temperate zones; evolution in *Campanula* involved the development of smaller spinules and increasing numbers of pores as well (Dunbar, 1975b). In the Lobelioideae colpate grains occur in *Laurentia* and *Lobelia* (Lobelieae), and colporate types occur in six other genera examined (including one genus of Delisseeae). The sexine pattern and apertures of *Platycodon grandiflorus* evidently resemble those of some species of *Campanula* (including *C. persicifolia*) rather closely, indicating an affinity between these two genera (Dunbar, 1975b). Data on pollen morphology substantiate the contention that genera within the Campanuloideae remain poorly defined and that *Campanula* in particular is still rather heterogeneous, despite the segregation of many genera (Dunbar, 1975b).

Palynological evidence agrees with that provided by macromorphology regarding the intermediacy of the Cyphioideae, although according to Dunbar (1975b) it also suggests that they are more closely related to the Lobelioideae (as indicated by sexine patterning in particular). Nevertheless, Chapman concluded that these three subfamilies are poorly distinguished palynologically.

Dunbar (1975b) argued that palynologically the Campanulaceae appear to be more similar to the Goodeniaceae than to the Sphenocleaceae. The tectum of both *Cyananthus* (Campanulaceae) and *Scaevola* (Goodeniaceae) is uniformly punctate, although neither the aperture type ("lalongated os") nor the variable sexine thickness in *Scaevola* is seen in the Campanulaceae. The grains of *Sphenoclea zeylanica* have smooth surfaces (although Cronquist reported that they are reticulate), with protrusions of various sizes distributed in a pattern unlike any seen in the Campanulaceae.

The ovule in the Campanulaceae is unitegmic, anatropous, and tenuinucellar (the usually single archesporial cell becomes the megaspore mother cell, although instances of more than one archesporial cell per ovule have been reported in *Campanula* [Rosén, 1949]). The megagametophyte is of the Polygonum type and usually develops from the chalazal megaspore of a linear tetrad (Davis). However, development of nonchalazal megaspores and the occurrence of T-shaped tetrads have been observed in *Wahlenbergia* (Subramanyam, 1948). The synergids are hooked in *Wahlenbergia* and other genera (Subramanyam, 1948), and a filiform apparatus has been reported in *Campanula* (Barnes) and *Lobelia* (Davis). Of the 295 families for which such information is available, 56 demonstrated both of these characters. Nevertheless, neither occurs throughout a given family, suggesting that their taxonomic significance may lie below this level (Davis). Starch grains are present in the embryo sac of *Campanula* and *Wahlenbergia,* among others (Davis).

Endosperm formation is *ab initio* cellular, although its development is of three different types (Rosén, 1949): Codonopsis type (e.g., in *Campanula, Wahlenbergia, Lobelia*), Phyteuma type (e.g., in *Campanula, Triodanis, Laurentia* [Lobelioideae]), and Sphenoclea type (in *Sphenoclea*). (It is notable that the Phyteuma type was considered transitional to a fourth type, found in the Goodeniaceae.) Both micropylar and chalazal haustoria occur throughout the family, as does the Solanad type of embryogeny (Davis). Polyembryony has been observed in *Jasione, Wahlenbergia, Lobelia,* and others. The seeds are small and exarillate. According to Corner, the exotestae are composed either of cuboid or fibriform cells, although the taxonomic significance of this in the Campanulaceae was not indicated.

The economic significance of the Campanulaceae lies chiefly in its relatively large number of attractive ornamentals. Species of many genera, including all those represented in the Southeast, are often favored by gardeners (see Bailey *et al.,* Bailey & Lawrence, Crook). A number of species, particularly of *Lobelia,* have been of medicinal and/or other value as well (see discussions and bibliographies of genera).

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KEY TO THE GENERA OF CAMPANULACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *herbs with latex; leaves simple, usually alternate, exstipulate, sessile to petiolate, margins various, sometimes lobed; flowers in inflorescences (rarely only 1 or a few per plant), perfect, sometimes cleistogamous, often showy, sometimes bracteolate, actinomorphic or zygomorphic, proterandrous; hypanthium sometimes extended above ovary; calyx synsepalous, usually 5-lobed (often with a reflexed appendage in the sinuses between lobes), persistent in fruit; corolla sympetalous, lobes usually 5 and alternate with the calyx lobes; stamens equal in number to and alternate with the corolla lobes, filaments sometimes connate above, anthers forming a tube (either by coherence or connation) into which pollen is shed and from which the pollen is removed by elongation of the style; gynoecium usually 2- or 3-carpellate, syncarpous, ovary inferior or half-inferior and often bearing an annular nectariferous disc, the locules usually equal in number to the carpels; ovules numerous in each locule on mostly axile placentae, anatropous, unitegmic; fruit a capsule, dehiscent apically or laterally; seeds numerous, small.*

A. Corollas actinomorphic or nearly so; anthers free or coherent in a tube around the style, becoming free after anthesis; staminal filaments free; carpels usually 3; flowers not resupinate.
  B. Capsules dehiscent apically (within the calyx lobes); flowers solitary (or nearly so), in compact umbels, or in open inflorescences (and leaves then sessile and at least the lower ones entire, undulate, and/or remotely and finely serrate; anthers free and caducous; styles not conspicuously exserted).
    C. Flowers/fruits in an (involucrate) umbel. . . . . 4. *Jasione.*
    C. Flowers/fruits not in an umbel.
      D. Flowers small, numerous, arranged in an open inflorescence; plants often much branched (sometimes from the base); leaves small, linear to narrowly elliptic, if serrate only remotely and finely so. . . . . 3. *Wahlenbergia.*
      D. Flowers large, 1 to few, solitary or nearly so; plants often unbranched (never branched from the base); leaves large, ovate to elliptic, serrate. . . . . [*Platycodon*; see footnote 5.]
  B. Capsules dehiscent laterally; flowers in spikes or in open inflorescences (and most leaves then petiolate or at least constricted at base and at least lower ones coarsely serrate, very rarely remotely and finely serrate; anthers coherent and persistent; styles conspicuously exserted).
    E. Inflorescence branched, or if spicate the flowers pedicellate, corollas campanulate, or if rotate the styles upcurved; leaves usually petiolate; cleistogamous flowers lacking; capsules obconical to subglobose. . . . 1. *Campanula.*
    E. Inflorescence spicate, flowers sessile, corollas rotate, styles straight; leaves sessile; cleistogamous flowers present (at lower nodes); capsules narrowly cylindrical. . . . . 2. *Triodanis.*
A. Corollas zygomorphic; anthers connate in a tube around the style, not becoming free after anthesis; staminal filaments connate above; carpels 2; flowers resupinate. . . . . 5. *Lobelia.*

Subfam. CAMPANULOIDEAE [Schönland, Nat. Pflanzenfam. IV. **5:** 48. 1889]

Tribe CAMPANULEAE [Endlicher, Gen. Pl. 516. 1838]

1. **Campanula** Linnaeus, Sp. Pl. **1:** 163. 1753; Gen. Pl. ed. 5. 77. 1754.

Erect, suberect [or rosette- or mat-forming], perennial or sometimes annual [or biennial] herbs. Leaves alternate, sessile to petiolate, entire or dentate, sometimes lobed. Inflorescences racemes or panicles, sometimes spikes [or heads, or flowers solitary]; flowers perfect. Calyx actinomorphic, the tube ovoid or subglobose, 5-lobed, needle shaped to triangular, often with a reflexed lobe or appendage in each sinus, commonly longer than the tube. Corolla actinomorphic, rotate, campanulate, or funnelform, lobes 5. Stamens 5, epipetalous; filament strongly to weakly dilated at the often-persistent base; anther elongate. Ovary inferior, locules 3–5; placentation axile; stigma lobes 3–5. Fruit an ovoid to turbinate capsule, often strongly ribbed, dehiscent by 3–5 lateral pores or valves [rarely indehiscent]; seeds brown, lustrous, ellipsoid, turgid or flattened. (Including *Rotantha* J. K. Small, 1933, not J. G. Baker, 1890, and *Campanulastrum* J. K. Small, 1903.) LECTOTYPE SPECIES: *C. latifolia* L.; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **3:** 294. 1913. (*Campanula* listed by Linnaeus [Philosophia Botanica, p. 142. 1737] as a name provided by Tournefort. Name from Latin *campana,* a bell, referring to the shape of the corolla, and *ula,* diminutive.)—BELLFLOWER.

The largest genus in the Campanuloideae, consisting of over 300 species (more than 500, according to Contandriopoulos) and mostly confined to the North Temperate Zone. The plants occupy a variety of habitats (e.g., deserts, forests) but are most frequent and most diverse at high elevations. Relatively large numbers of species occur in the Caucasus and eastern Mediterranean regions, as well as in the mountains of western Europe. There are about 150 species in the Soviet Union (Fedorov) and some 144 in Europe (Fedorov & Kovanda in Tutin). About 20 species are native to North America (Shetler, 1963).

Despite the segregation of a number of genera (including *Platycodon* and *Triodanis*) from *Campanula,* doubts regarding its homogeneity persist. In addition, although most species of *Campanula* are fairly well marked, infrageneric relationships (i.e., species groupings) are obscure. Two initial classifications (A. de Candolle, Boissier) were rather conflicting, and although each has been shown to be mostly unnatural, no modern alternatives based on world-wide study have been published. It is almost universally agreed among students of the group that a modern revision is long overdue; most investigators have indicated that a successful treatment must incorporate cytology, seed morphology, capsule dehiscence, life form, and geography.

Alphonse de Candolle divided *Campanula* into two sections based on the presence (sect. *Medium* A. DC.) or absence (sect. *Eucodon* A. DC. [= sect. *Campanula*]) of appendages between the calyx lobes. Although his treatment is still of value (it is the only treatment on a worldwide basis), species that do not fit in either section have subsequently been described. Boissier considered the nature of capsule dehiscence to be of greater taxonomic value, and on that basis he proposed two sections with different circumscriptions. Species in De Candolle's sect. *Eucodon* with dehiscence near the top of the capsule were removed to sect. *Rapunculus* Boiss., while the remaining species (including the type of the genus) were united with sect. *Medium* A. DC. to form a group in which dehiscence was basal. Most subsequent treatments, including that of Schönland, have followed the system of Boissier, even though it is generally regarded to be as artificial as that of De Candolle. In the *Flora of the U.S.S.R.,* Fedorov recognized the two sections of Boissier but further divided them into subsections and series that are in most cases more natural than the sections. Damboldt's treatment for the *Flora of Turkey* largely follows that of Fedorov, except that many of Fedorov's infrageneric taxa are elevated in rank. (Damboldt recognized six subgenera and numerous sections.)

Numerous cytological studies have provided data bearing on the infrageneric relationships of *Campanula.* Sugiura concluded from evidence obtained from over 70 species that the genus is composed of two main groups. Those species with a gametic chromosome number of eight (or some multiple of eight) evidently have linear-lanceolate leaves, while those with 17 (or some multiple of 17) have wider leaves.

Gadella (1964) showed that De Candolle's sect. *Medium* is rather homogeneous cytologically: 19 of 21 species with appendaged calyces have $2n = 34$, although many (but not all) of the exappendiculate species comprising De

Candolle's sect. *Eucodon* were also found to be of this cytotype. Boissier's sections, on the other hand, were considered to be cytologically heterogeneous. Sugiura's proposal of two groups differing in base chromosome number and leaf shape was regarded as untenable by Gadella, who (for reasons that do not appear to be completely justified) indicated instead that a classification based on a combination of characters, including chromosome length and base number, basal leaf shape, and location of capsule dehiscence, seemed justified. Accordingly, Gadella established seven informal groups of species that differ in base chromosome numbers. Since a majority of the species of *Campanula* were not considered and the relationships involved were unclear, the arrangement was considered provisional.

The chromosome numbers characterizing some of Gadella's groups have been determined subsequently in more distantly related species; in some cases the same number has been differently and independently derived as well. Nevertheless, Contandriopoulos considered Gadella's approach to be well founded and proposed a phylogeny based on cytology, morphology, life cycle, and geographic distribution that reflected the exceedingly complex cytotaxonomy of *Campanula* and suggested how Gadella's groups might be interrelated. The base chromosome numbers 5, 6, 7, 8, and 9 were considered to be primary; 8 was thought to be the ancestral number, perhaps evolved independently of 9 but more directly linked to the others. A secondary base number, 17, is characteristic of a great many species in the genus (and in the family as well—several genera have only species with this number). Contandriopoulos rejected the idea that $x = 17$ resulted from amphiploidy involving plants with either $x = 7$ and $x = 10$ or $x = 8$ and $x = 9$ and accepted as plausible the hypothesis of Böcher (1960), who considered 17 to have resulted from a single trisomy in the $2n = 16$ cytotype (see, however, Sugiura; Gadella, 1963, 1964).

Fedorov's classification of *Campanula* is usually considered to be the most natural, apart from the questionable division of the genus into two sections based on the location of capsule dehiscence. Gadella (1964) regarded it as artificial only for those subsections between which members had been successfully hybridized (by him). Since only two of our species, both naturalized in the Southeast, are from the Old World, application of Fedorov's system to the others is unclear. With the possible exception of *C. Robinsiae* Small, the species indigenous to our area are restricted to North America and are probably unrelated to any in the Old World.

The most recent enumeration of the North American species of *Campanula* was provided by Shetler (1963). Of the 20 native species, 16 were indicated to be endemic to a portion of the continent, two were amphi-Atlantic, and two were circumpolar. Three European species (excluding *C. persicifolia* L., below) were considered to have escaped from cultivation and to have become naturalized in (unnamed parts of) North America.

Three or four species (depending on taxonomic interpretation) of *Campanula* are indigenous in the Southeast, while the origin of *C. Robinsiae* has yet to be resolved.

Campanula Robinsiae differs from other species of the southeastern United States, with the exception of the very distinctive *C. americana* L., in its annual habit. Although initially considered to be endemic to a small area in Florida, its status at present is uncertain. The area in which it occurs—wet, grassy slopes of Chinsegut Hill, near Brooksville, Hernando Co., Florida, an area long disturbed by cultivation—is not especially known for local endemics (Shetler, 1963). Its similarity to *C. Reverchonii* Gray, an annual species endemic to granitic soil in the Llano region of the Edwards Plateau in Texas, was noted by Small (1926) and by Shetler (1963). However, Ward pointed out that such a distribution is not duplicated by other species pairs and summarized arguments that *C. Robinsiae* most likely represents a recent introduction from the Old World. Morin (pers. comm.) recently collected *C. Robinsiae* from wet places in the Brooksville area (some plants submerged). She considered it to be unrelated to any other North American species of *Campanula,* in part because in her material the pollen had bifurcate spines on the surface and the seeds in cross section were triangular with protuberances on the angles. The annual habit, the low, divaricately branched, leafy stems, the absence of rosettes, and the basal capsule dehiscence suggest to me that its affinities may lie with species belonging to subsect. *Annuae* (Boiss.) Fedorov and native to the Caucasus and Mediterranean regions.

Campanula aparinoides Pursh, $2n = 34$, 136, 170, and *C. floridana* S. Watson ex Gray are closely related. Indeed, Shetler (1963) recognized the possibility that *C. floridana,* an endemic of peninsular Florida, is merely a southern race of the more widespread *C. aparinoides,* which has not been recognized in Florida but is found in the northeastern part of our range. Both are plants of swamps, marshes, and peatlands and have weak, slender, reclining stems—features that separate them from all other southeastern species of *Campanula. Campanula aparinoides* differs from *C. floridana* in its (usually) retrorsely scabrous stems and leaves and its campanulate or funnelform (vs. more rotate) corollas that are rarely divided below the middle (vs. divided almost to the base) into wide (vs. narrow) lobes. *Campanula aparinoides* is generally considered to be endemic to the eastern and central United States and adjacent Canada but has recently been reported from Wyoming, apparently as a native (Lichvar & Dorn). The position of these species in Fedorov's system is not clear, although A. de Candolle included *C. aparinoides* (and *C. divaricata,* below) in a group of 22 species that also included *C. rotundifolia* L., $2n = 68$, a species placed by Fedorov in subsect. *Heterophylla* (cited as subsect. *Heterophylla* (Nyman) Fedorov by Fedorov; see, however, Geslot) (flowers drooping, calyces exappendiculate, capsules dehiscing at the base). *Campanula aparinoides* qualifies on cytological grounds for inclusion in Gadella's group VII, a heterogeneous assemblage that included species in many of Fedorov's subsections, including subsect. *Heterophylla.* Among the indigenous species of *Campanula* in the Southeast, *C. aparinoides* may bear a relationship to *C. rapunculoides* L., $2n = 68$, 102, of subsect. *Campanula* (stems tall, simple; inflorescences many flowered, racemose; calyces exappendiculate; capsules pendulous, dehiscing near the base). Although *C. floridana* and *C. Robinsiae* were placed by Small in his genus *Rotantha,* the species are clearly unrelated.

Campanula divaricata Michaux (*C. flexuosa* Michaux[7]), $2n = 40$ (34 according to Gadella, 1964), is an erect plant with profusely branched panicles, small, shallowly incised corollas with recurved lobes, and conspicuously exserted styles. It generally occurs at low elevations in the Appalachians, on cliffs (often in small crevices), in dry rocky woods, and along waysides. Endemic to an area from Maryland south to Georgia and Alabama, it rarely is an adventive farther north (Shetler, 1963). Pease reported that a single individual persisted naturally in New Hampshire at least from 1920 to 1960 without reproducing sexually. *Campanula divaricata,* like most other North American endemics in the genus, is largely confined to unglaciated regions. It is therefore thought to have survived south of the limit of glaciation. Contandriopoulos indicated that species with $2n = 40$ belong to a lineage with $x = 5$ as the base number. This lineage appears to be monophyletic and unrelated to other lines, including those to which other southeastern species belong.

According to Shetler (1958) *Campanula americana* L., $2n = 58, 102$, has no close relatives in the genus. Its tall, robust habit, rotate, deeply cut corollas, and exserted, upcurved styles represent a unique combination of characters within the genus. Nevertheless, its separation by Small into the monotypic *Campanulastrum* was not initially supported by Shetler (1958; see, however, Shetler & Matthews) because the rotate corollas at least in part defining this genus do not occur in *C. americana* f. *tubulifera* Fern. and are found elsewhere in *Campanula.*[8] Shetler & Matthews favored recognition of *Campanulastrum* on cytological and palynological evidence, as did Gadella (1964, 1966b) on cytological and morphological grounds.

Shetler (1958) observed that plants of *Campanula Scouleri* Hooker, of the west coast of North America (Alaskan panhandle to northern California), are very similar to small, unbranched individuals of *C. americana* and suggested that the latter may represent diploids in a series in which larger, more typical plants are polyploids ($2n = 102$). However, Gadella (1964) reported a diploid number of 58 throughout *C. americana,* and the chromosome number of *C. Scouleri* has not been reported.

There has been some confusion about the duration of individuals of *Campanula americana.* The species has been reported as an annual (Cruden; Senior; Shetler, 1962; Steyermark), a biennial (Morin; Radford *et al.*; Shetler, 1963), or as an annual or biennial (Diggs; Small, 1933). Baskin & Baskin studied populations in an open secondary hardwood–*Juniperus virginiana* forest in Kentucky (Fayette Co.) and found a low-temperature vernalization requirement for flowering that could not be met in the seed stage. Since *C. americana* is monocarpic, it behaves either as a winter annual, if plants are from seeds that germinated in summer or fall, or as a biennial, if the seeds germinated in spring. The Baskins concluded that a relatively simple genetic change could result in

[7]Gray (Synopt. Fl. N. Am. **2:** 13, 14. 1878) was evidently the first to unite these species. His choice of *Campanula divaricata* must be followed in accordance with Article 57.2, ICBN, 1983.

[8]As Shetler (1958) has pointed out, Small must have had other characters in mind when he established the genus *Campanulastrum,* or he presumably would not have later erected the genus *Rotantha* for two other species with rotate corollas, *C. floridana* and *C. Robinsiae.*

a shift from one to the other life cycle, and that plants of the species may indeed behave differently in different populations.

Campanula americana is endemic to and widely distributed throughout eastern North America, where it occurs in partial shade in moist, rich, well-drained, usually calcareous soil. Although it is most common near streams and rivers, it is not restricted to alluvial conditions (Shetler, 1958). It evidently occurs throughout the Southeast, but its abundance appears to be correlated positively with elevation. It is clearly least frequent on the Coastal Plain and is less abundant in the Piedmont than in the adjacent mountains. In Florida it is restricted to the western part (the panhandle).

Fedorov included *Campanula persicifolia* L. and *C. Rapunculus* in subsect. *Campanulastrum* (Small) Fedorov. However, his designation of *C. Rapunculus* as the type of this subsection is incorrect because *C. americana* was the only species included in the genus *Campanulastrum* by Small and must, therefore, be considered the type. *Campanula americana* does not appear to belong to the group of Russian plants recognized by Fedorov.

Campanula rapunculoides, $2n = 68, 102$, is similar to *C. americana* in its coarse, erect habit and spicate inflorescences, but it differs in its secund inflorescences, campanulate to tubular corollas (rarely incised below the middle), included or barely exserted and never upcurved styles, and basal capsule dehiscence (vs. dehiscence near the top of the capsule). A native of Eurasia, *C. rapunculoides* is widely naturalized as an escape from cultivation. It occurs throughout the northeastern quarter of the United States and adjacent Canada (Newfoundland to North Dakota south to Maryland and Illinois) along roadsides and in waste-ground and yards. It is rare and of restricted distribution in the Southeast, where it is known with certainty only from Watauga and Avery counties in northwestern North Carolina. It is known from two counties in northern Missouri (Steyermark) and from one in southwestern Virginia, as well. In the southern part of its indigenous Old World range, *C. rapunculoides* has diverged into a series of intergrading races, but it is more uniform toward its northern limit at the forest-tundra ecotone (Fedorov). *Campanula rapunculoides* was placed by Fedorov in subsect. *Eucodon* (= subsect. *Campanula*) ser. *Rapunculoideae* Charadze, which differs from ser. *Latifoliae* (= ser. *Campanula*) in its smaller flowers and its curved or spreading (vs. straight) calyx lobes that are ⅕ to ¼ (vs. ⅓ to ½) as long as the corolla. Damboldt put *C. rapunculoides* in sect. *Quinqueloculares* (Boiss.) Phitos. Its possible relationship to *C. aparinoides* is discussed above.

Campanula persicifolia L., $2n = 16$ (some 17, 18, 32), superficially resembles *C. rapunculoides* but has narrower cauline leaves and more deeply trifid styles. A native of Europe, it has been reported as an escape from cultivation in North America in both western North Carolina (Small, 1933; but specimens substantiating this have not been located) and eastern Canada, where it is reportedly naturalized as well (Cinq-Mars *et al.*). Morin (pers. comm.) noted a specimen from Nebraska in the collections of the Missouri Botanical Garden, but neither she nor I have seen any material from the Southeast. The species was placed by Fedorov in subsect. *Campanulastrum* and by Gadella (1964) in his Group I. According to the scheme of Contandriopoulos, it is unrelated to other species

occurring in the Southeast. Artificial hybrids between *C. persicifolia* and the closely related *C. latiloba* DC. were sterile (Gadella, 1967).

The apparent absence from the Southeast of the extremely polymorphic and circumboreal *Campanula rotundifolia* L. is somewhat surprising, since it occurs throughout North America, with the most notable exception of the extreme Southwest and our area (Shetler, 1979b). It grows in Missouri in moist, shaded, north-facing crevices of limestone in the southeastern Ozarks (Shannon Co.) within about 40 miles of Arkansas (Steyermark), as well as in western Texas and parts of Mexico (Shetler, 1979b).

Pollen in *Campanula* is binucleate when shed (Brewbaker). It is generally spherical to suboblate (occasionally subprolate) and has three or four usually equatorial pores. Usually the surface bears spines that vary in size (particularly between species) and are superimposed on a fine reticulum. It is notable that pollen of *C. americana* has 12 pores distributed more or less equally over the entire surface of the grain and that in sexine pattern it is similar to that of *Wahlenbergia* and certain other genera of the Campanulaceae (Dunbar, 1975b).

An extensive literature dealing with the reproductive biology of *Campanula*, including a debate concerning the relative importance of autogamy in the genus, has been thoroughly reviewed by Shetler (1979a). Species of *Campanula* were often thought not to be insect pollinated and/or not to be allogamous, primarily because of the way in which the pollen is presented. While the flower is still in bud, the coherent anthers begin to shed pollen introrsely onto retractile hairs on the apical portion of the style. During anthesis pollen is carried aloft out of the anther tube as the base of the style elongates; the stigmas do not normally spread until all of the hairs and pollen grains have disappeared from the style. Nevertheless, the deposition of pollen on the style and the retraction of the trichomes have often been thought to constitute self pollination and to lead to self fertilization by growth of pollen tubes directly into the style. Other arguments for autogamy have pointed out that pollen release and stigma receptivity sometimes overlap in individual flowers (and that in such cases exiting insects could transport pollen from style to stigma), that pollen could fall from styles to stigmas in pendent flowers, and that recurving stigmas could eventually come in contact with the style. Autogamy could also be effected by insects in multiflowered species, since floral development is sequential. Despite these and other hypotheses that have generally not been supported by observation, most evidence indicates that cross pollination (and subsequent fertilization) by insects is the rule within the genus. (For a list of pollinators, see Knuth.)

The flowers of *Campanula* show adaptations usually associated with insect pollination, including blue or violet, campanulate or tubular corollas; nectar and a means of protecting it from visitors that do not enter the flower in a way likely to effect pollination (the broad, triangular filament bases form a dome over the nectary such that entrance to it can best be gained near the style after passage by pollen and stigma); proterandry; and echinate pollen. Gadella (1964) found that among 21 species tested, spontaneous self fertilization occurred in only two (including one population of *C. persicifolia*) when flowers were bagged, and that mature seeds were produced in only one of 18 species artificially self pollinated.

Narrower debates have centered on the adaptive significance of the method of pollen presentation in *Campanula,* and in particular on the fact that the collecting hairs retract. The mechanism of presentation may prevent pollen gathering by nonpollinating visitors, and/or it may insure that pollen is deposited on pollinators in places most likely to come in contact with stigmas of the same species, thus contributing to pollen economy and perhaps to reproductive isolation as well (Brantjes). It seems clear that the hairs serve to hold the pollen in place as it is removed from the anther tube, but it has been suggested that they may also help in the exit of small insects from the corolla.

The retraction of the collecting hairs, a feature probably unique to the Campanulaceae, involves an invagination of the apical portion of each hair into its basal portion that is thought to be irreversible and osmotically induced (see Shetler, 1979a). Although this may be a mechanism by which pollen is brought into contact with the stylar tissue, it has been shown that the hairs do not function in this way and that pollen tubes are only able to penetrate the style through the stigmatic surfaces. The lack of evidence for spontaneous autogamy also argues against stylar pollination and, therefore, against the proposal that retracting hairs help to bring it about.

Retraction of the collecting hairs is not likely to facilitate pollen release to visiting insects and does not result from mechanical stimulation (but see Carolin, 1960), although pollen removal and hair retraction are simultaneous and do not occur to any great extent in the absence of insect visitors. Nevertheless, the hairs probably enhance the likelihood of pollination by holding pollen on the style in the path of nectar-seeking visitors. Retraction, therefore, may be of no real significance, but simply the consequence of some physiological change perhaps brought about by the pollinator.

Many species of *Campanula,* especially those with large flowers (e.g., *C. americana, C. persicifolia, C. rapunculoides*), are cultivated for their ornamental value, and some, including *C. americana,* have been investigated as sources of latex in the production of rubber (Buchanan *et al.,* 1978a, 1978b).

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2. **Triodanis** Rafinesque, New Fl. Bot. N. Am. **4:** 67. 1838.[9]

Erect or ascending (sometimes reclining), terrestrial, annual herbs. Stems simple to much branched, usually at or near the base; when pubescent the trichomes nonglandular, often retrorse, and largely confined to membranaceous, longitudinal ridges. Leaves alternate, often ciliate, sessile or sometimes

[9]Barnhart (Torreya **7:** 177–182. 1907) showed that the publication date of this work was 1838, not 1836 as the cover indicates.

petiolate near base of plant; blade broadly ovate, elliptic, or linear, the base attenuate, cuneate, obtuse, truncate, or auriculate, sometimes clasping the stem, the apex acuminate to obtuse, sometimes mucronate, the margin entire or crenate, each tooth strongly asymmetric and often mucronate. Inflorescences appearing loosely spicate, with lower flowers usually cleistogamous (and then often with missing or rudimentary parts). Flowers sessile, actinomorphic, usually 1 per axil and terminating a repressed axillary branch [or more numerous (2 or 3, rarely to 8) when the axillary branch elongates (and sometimes branches)], sometimes subtended by a bract. Calyx actinomorphic; tube ellipsoid to narrowly ellipsoid; lobes usually 5, but sometimes 3 or 4 in cleistogamous flowers, entire, usually ciliate, attenuate, persistent in fruit. Corolla actinomorphic; tube funnelform; lobes usually 5, longer than the tube, usually about twice as long as wide, lanceolate to elliptic [or broadly ovate and abruptly acuminate], apex obtuse or attenuate. Stamens usually 5, epipetalous, rudimentary in cleistogamous flowers; filament short, flattened; anther linear, longer than the filament. Ovary inferior, locules 3 (sometimes 2; 1 in *T. leptocarpa*); placentation axile to subparietal (sometimes in individual ovaries) (parietal in *T. leptocarpa*); style rudimentary in cleistogamous flowers; stigma lobes equal in number to the locules. Fruit an ellipsoid to narrowly ellipsoid, sometimes clavate capsule (subulate in the cleistogamous flowers of *T. leptocarpa*), dehiscent by lateral pores equal in number to the locules of the ovary (except sometimes in *T. leptocarpa*); seeds mostly tan or dark brown, usually longer than wide, turgid or flattened, essentially smooth. (Excluding *Specularia* Heister ex A. DC., 1830, = *Legousia* J. F. Durande, 1782.) LECTOTYPE SPECIES: *T. rupestris* Raf. (= *T. perfoliata* (L.) Nieuwl.); see McVaugh, Wrightia **1**: 23. 1945. (According to Rafinesque, the name means "three unequal teeth," in reference to the calyx lobes [which in fact are only sometimes unequal].)

A small genus of perhaps six or seven North American and one Mediterranean–Middle Eastern species that has gained acceptance only in relatively recent times. *Specularia* Heister ex A. DC. (= *Legousia* J. F. Durande), a group of about seven species segregated primarily from *Campanula,* was generally recognized until McVaugh (1945b) pointed out that it could not in its traditional circumscription be logically maintained apart from *Campanula.* McVaugh proposed, however, that if *Specularia* were restricted to the type (and perhaps one other species), and if the intermediate *S. pentagonia* (L.) A. DC. were transferred from *Specularia* to *Campanula,* relatively homogeneous units, including *Triodanis,* would result. Although Fernald rejected this arrangement and chose to retain *Specularia,* maintaining that there were too many qualifications to the generic differences enumerated by McVaugh, he did not address McVaugh's main argument (i.e., that if *Specularia* were segregated from *Campanula, Triodanis* must also be). McVaugh's rebuttal (1948) further strengthened his case, and *Triodanis* is recognized here. A combination of characters (including annual habit, deeply divided corolla, capsules that are longer than wide and open near the apex [but see below], spicate inflorescences, and regular production of cleistogamous flowers at the lower nodes) is unique and defines *Triodanis* in the sense of McVaugh (1945b).

Four or five species of *Triodanis* occur in the Southeast. *Triodanis perfoliata*

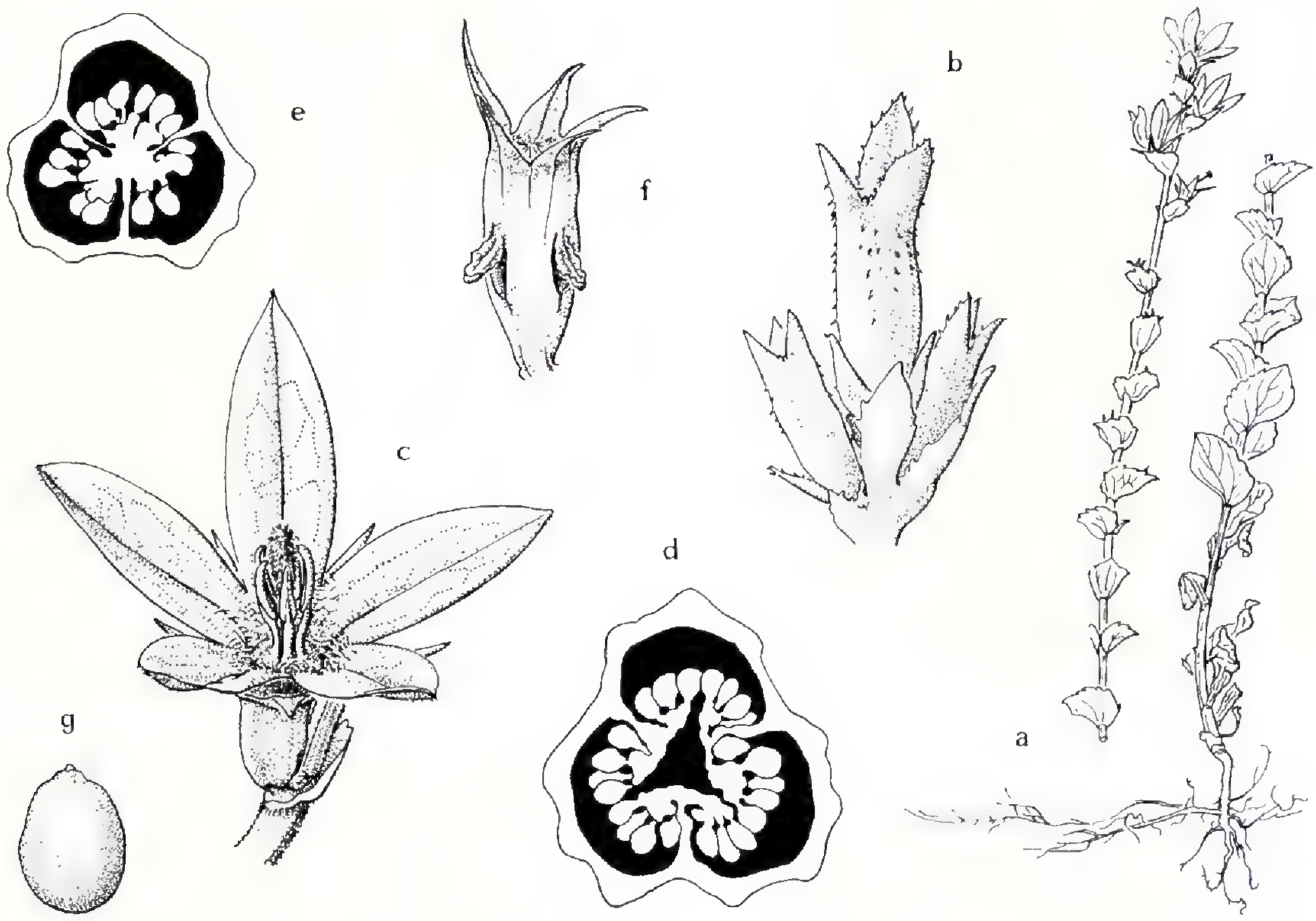

FIGURE 1. **Triodanis.** a–g, *T. perfoliata:* a, small plant, inflorescences in leaf axils appearing single flowered, × ½; b, axillary inflorescence with 3 cleistogamous flowers visible, each with 3 calyx lobes, the largest flower with 2 bracteoles visible, × 8; c, chasmogamous flower with subtending bract removed, × 4; d, cross section through apical portion of ovary (placentation intermediate between axile and parietal, the latter characteristic of *T. leptocarpa*), × 15; e, cross section through basal portion of ovary, × 15; f, capsule with persistent calyx lobes, lateral dehiscence, × 4; g, seed, × 30.

(L.) Nieuwl. (*Specularia perfoliata* (L.) A. DC.) and *T. biflora* (Ruiz & Pavon) Greene (*Specularia biflora* (Ruiz & Pavon) Fischer & Meyer), each $2n = 56$, are quite similar morphologically and may be conspecific (see below). The most common species of the genus in our area, *T. perfoliata* has—as compared with *T. biflora*—dehiscence near or below the middle of the capsule (vs. near the top), bracts that are wider than long (vs. longer than wide), and several (vs. one or two) inflorescences with chasmogamous flowers. Both species are widespread in the Southeast, although in North America *T. biflora* appears to have a more southerly distribution. It is therefore interesting that, although McVaugh (1945b) considered *T. biflora* to be native in many parts of South America, he suggested that *T. perfoliata* may have been introduced there (except perhaps in Ecuador, where it may be native). Both species occur in a variety of natural and disturbed habitats, with the exception of deserts and places with permanently wet ground. McVaugh (1943) considered *T. perfoliata* to be more abundant and to behave more like a native species than *T. biflora* on granitic flat rocks in the Southeast.

Triodanis lamprosperma McVaugh, *T. texana* McVaugh, and *T. Holzingeri* McVaugh are very similar in general appearance to the two preceding species. *Triodanis lamprosperma* is easily distinguished by its large (greater than 0.8

mm wide), flatly lenticular, smooth, highly polished seeds. It occurs in a variety of habitats in Louisiana, western Arkansas, southern Missouri, and eastern Oklahoma. *Triodanis texana,* with quadrangular, roughened seeds, occurs mostly in sandy soils in woods, pinelands, and plains and has a distribution in eastern Texas that closely approaches southwestern Louisiana. (It is evidently unknown from our area.) *Triodanis Holzingeri,* distinguished from the preceding species by linear (vs. broadly elliptic to rounded) capsule openings, occurs in prairies in the central United States. Although McVaugh (1945b) reported an outlying station in southwestern Tennessee, I have seen no specimens of this species from the Southeast.

Triodanis leptocarpa (Nutt.) Nieuwl. is easily recognized by its lanceolate to linear leaves subtending the axillary inflorescences (often appearing as flower bracts in the case of one-flowered inflorescences) and its long, narrow capsules with openings near the top. It is a prairie plant of the central United States that enters our area in western Arkansas and Louisiana. *Bradley 3281* (NY), from a roadside in Missouri, is intermediate between *T. leptocarpa* and *T. perfoliata* in the shape of leaves subtending inflorescences and in the position of capsule openings.

Cytological evidence supports the recognition of *Triodanis* (Gadella, 1966b) in that both *Specularia speculum* A. DC. (the type of *Specularia*) and *S. pentagonia* (L.) A. DC. (an enigmatic species returned to *Campanula* by McVaugh [1945b]) are $2n = 20$, while *Triodanis falcata* (Ten.) McVaugh (Mediterranean region) is $2n = 26$ and *T. perfoliata* and *T. biflora* are $2n = 56$. These data also suggest that two infrageneric taxa may be recognizable in *Triodanis,* one comprising *T. falcata* and the other made up of the New World species.

Gray proposed that the American species of *Triodanis* were divisible into two sections based primarily on placentation and capsule shape. Accordingly, he placed *T. biflora* (placentation axile, capsules elliptic) in one and *T. leptocarpa* (placentation parietal, capsules narrowly elliptic) in the other. It is notable that in *T. perfoliata* placentation in a single ovary may grade from nearly parietal in the upper part to axile toward the base (FIGURE 1d, e), suggesting that the proposed sections of Gray are untenable.

Bradley scored individuals of *Triodanis perfoliata* and *T. biflora* obtained from natural populations in the Southeast and grown under uniform conditions, as well as the offspring resulting from various crosses involving these plants (selfing, F_1 and F_2 hybrids, and backcrosses to both parents), for each of the characters mentioned above. Since a range of values extending from one extreme to the other was obtained for each character and since the hybrids were fertile, Bradley considered the plants involved to be conspecific. However, because of the persistence, despite interbreeding, of the combination of three traits characterizing *T. biflora* (which Bradley attributed to linkage and the high degree of self fertilization resulting from low numbers of chasmogamous flowers), he chose to recognize this taxon as *T. perfoliata* var. *biflora* (Ruiz & Pavon) Bradley. Ward, however, rejected this view and chose instead to maintain the species as distinct because other workers had not expressed difficulty in separating them and because his own observations revealed few or no intermediates. Ward also indicated that isolating mechanisms were clearly op-

erating in the field and that treating these taxa as varieties would constitute too great an expansion of the original meaning of that rank.

The inflorescence characters discussed above have been found to be susceptible to environmental modification. Data obtained by Trent (1940b) for *Triodanis perfoliata* indicated that, although cleistogamous and chasmogamous flowers increased in number at equal rates with increasing photoperiod, chasmogamous flowers increased more quickly than cleistogamous ones with increasing light intensity. Since in both cases cleistogamous flowers outnumbered chasmogamous ones, the proportion of all flowers that were chasmogamous was greater when both photoperiod and light intensity were increased. Bradley reported that while the number of chasmogamous inflorescences in *T. perfoliata* could be reduced to two by poor habitat conditions, *T. biflora* produced only two even under good conditions.

The structure of the flower in *Triodanis perfoliata* is extremely variable (Trent, 1940a). Among chasmogamous flowers sepals, petals, and stamens vary in number (two to seven sepals, one to six petals, and one to six stamens) and include both normal and vestigial parts, while the ovary is consistently three-locular. Cleistogamous flowers are less variable (three to six sepals, three to five petals, and one to five stamens), with sepals always normal, petals always vestigial, and stamens either normal or vestigial; the ovary is either two- or three-locular.

Trent (1942) compared the anatomy of cleistogamous and chasmogamous flowers of *Triodanis perfoliata.* The ovules and seeds of both were found to conform to the types seen throughout the Campanulaceae, although chasmogamous flowers were determined in general to produce more ovules (80–290) than cleistogamous ones (31–180). Each type of flower was found to produce both binucleate and (less frequently) trinucleate pollen, but differences in pollination were reported. Fertilization was observed in chasmogamous flowers in a few instances but never in cleistogamous ones, in which some evidence for parthenogenesis was reported (pollen grains were observed to germinate within the anthers and to grow through the anther wall but only as far as the adjacent stigma). Although embryo development in *T. perfoliata* appeared to conform to the "Capsella type" (= Crucifer type?), something closer to what is usually termed the Solanad type (characteristic of the Campanulaceae) was described (the basal cell results in a suspensor of 5 or 6 cells). Triple fusion may or may not occur, and endosperm development was reported to be the walled (= cellular) type. Finally, a greater percentage of seeds germinated from chasmogamous flowers than from cleistogamous ones (47.5 percent vs. 0.07 percent), while ungerminated seeds from both types of flowers usually had endosperm but no embryo, indicating that endosperm may have developed without fertilization.

Species of *Triodanis* are easily propagated, evidently either by seed or vegetatively, and are sometimes grown in flower gardens (Bailey *et al.*).

References:

Under family references see Bailey *et al.,* Chittenden, Gadella (1966b), Greene & Blomquist, Mark, McVaugh (1945b), Oosting & Anderson, Taylor, and Ward.

Under *Lobelia* see MIRANDA & SHARP. Note that the correct name of *Specularia* is *Legousia* and that *Specularia biflora* = *Triodanis biflora* and *S. perfoliata* = *T. perfoliata.*

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Tribe WAHLENBERGIEAE Endlicher, Gen. Pl. 514. 1838.

3. **Wahlenbergia** Schrader ex Roth, Nov. Pl. Sp. 399. 1821, nom. cons.[10]

Erect [ascending, prostrate, or caespitose], terrestrial, perennial [sometimes annual], [rhizomatous] herbs (sometimes woody toward the base) [or shrubs].

[10]According to Rickett & Stafleu (Taxon **9:** 122. 1960), *Wahlenbergia* was published by Schrader as a nomen nudum.

Stems several, branched or less frequently simple, often weak and divaricate, pubescent [rarely glabrous], [leaf scars distinct in woody species]. Leaves alternate [rarely opposite], sparser and smaller acropetally, sessile [sometimes subpetiolate or petiolate]; blade elliptic or lanceolate to linear or linear-subulate, glabrous or glabrate adaxially and pubescent to glabrate (with hairs confined to midrib) abaxially, the margin thickened (by hypodermal sclerenchyma visible as a white rim), shallowly dentate to entire [or rarely lobed]. Inflorescences cymose, open, branches alternate and terminated by a single flower or a cymule, bracts narrow; flowers perfect. Calyx actinomorphic; tube hemispheric to oblong-obconical; lobes 5 [rarely 3, 4, or 6], erect, linear. Corolla actinomorphic, funnelform; lobes 5 [rarely 3, 4, or 6], spreading, as long as to twice as long as the calyx lobes. Stamens 5 (rarely 3 or 4), free from the corolla, shorter than the style; filament membranaceous, broadened at the base; anther narrow, caducous. Ovary inferior, semi-inferior [or nearly superior], locules 2–4[–5]; placentation axile; stigma lobes [2 or] 3[–5]. Fruit a turbinate, hemispheric, or elongate cylindrical capsule, dehiscent by 2 or 3 apical pores; seeds amber colored, oblong, lenticular, lustrous. (*Cervicina* Delile, 1813, nom. rejic.) TYPE SPECIES: *W. elongata* (Willd.) Schrader ex Roth, nom. illeg. (*Campanula elongata* Willd., nom. illeg.) = *W. capensis* (L.) A. DC. (*Campanula capensis* L.). (Named for Georg Wahlenberg, 1780–1851, Swedish botanist.)

A genus of 100–220 species, an ambiguity due in part to its uncertain circumscription. *Wahlenbergia* is primarily distributed in the Southern Hemisphere, where it is generally considered to have undergone a development parallel to that of *Campanula* in the Northern Hemisphere. Three groups of species in *Wahlenbergia* were identified by Lothian (1947a) as being geographically and morphologically distinct, but these appear to have remained unnamed, as well as unrecognized, by other workers. The largest of these groups (ca. 90 spp., mostly perennial shrubs), considered to be centered in southern Africa, was thought by Lothian to have evolved from European members of *Campanula* and to have given rise to two smaller groups, one (ca. 20 spp., mostly perennial shrubs) in South America and another (ca. 10 to 12 spp., perennial or annual herbs) in Australasia.

Ecologically, *Wahlenbergia* is extremely variable. The four or five Australian species occupy a wide variety of habitats including xeric ones (Lothian, 1947b), while *W. hederacea* (L.) Reichenb. (Denmark to Spain and Portugal), for example, is a plant of damp, acid, peaty places on moors, heaths, and stream sides (Clapham *et al.*). *Wahlenbergia confusa* Merr. & Perry of New Guinea occurs between 3500 and 4000 m, while other species grow at or near sea level (Tuyn *in* Moeliono & Tuyn).

Wahlenbergia is usually placed in the Campanuloideae. In most systems it is near *Jasione*, and in some of these near *Platycodon* as well. It was, for example, included by A. P. de Candolle with 12 other genera (including *Jasione* and *Platycodon*) in the Wahlenbergieae Endl., a tribe characterized by apical dehiscence of the capsules. Schönland's segregation of *Platycodon* (carpels alternate with the sepals) from *Wahlenbergia* and *Jasione* (carpels opposite the sepals, at least when equal in number to them) is essentially recognized here, except that the subtribe Wahlenbergiinae Schönl., including *Wahlenbergia* and

Jasione, is treated as the tribe Wahlenbergieae Endl., which also included *Platycodon* (the Platycodinae Schönl. have not, to my knowledge, been recognized at the tribal level; see also family discussion). *Wahlenbergia,* sensu stricto, is evidently most closely related to *Cephalostigma* A. DC. (about seven species in tropical Africa, the East Indies, Brazil, and Peru [Schönland]) and *Lightfootia* L'Hér. (nearly 40 species in southern Africa and one each in Ethiopia and the Mascarene Islands [Schönland]). In fact, there appears to be growing support for the unification of these three genera under *Wahlenbergia,* sensu lato[11] (for a review of the problem by supporters of this unification, see Tuyn in Moeliono & Tuyn, Thulin).

Wahlenbergia is distinguished from other campanulaceous genera by a combination of traits, including flowers mostly actinomorphic, stamens free from the corolla, and capsules dehiscing by loculicidal, apical (i.e., within the calyx lobes) valves (vs. lateral dehiscence in *Campanula* and *Triodanis*). Alphonse de Candolle recognized six sections in *Wahlenbergia,* sensu stricto, based on habit, inflorescence characters (including peduncle length), the number of locules per capsule, and seed-surface texture. Three of these sections were further divided, and three were monotypic. Augustin P. de Candolle later elevated sect. *Edraiantha* to the generic level (often *Edraianthus* as a genus); transferred *Codonopsis* A. DC. to *Wahlenbergia* sect. *Megasanthes* (D. Don) A. DC.; combined sect. *Nesophila* A. DC.[12] with sect. *Aikinia* A. DC.; established sect. *Phyteumoides* A. DC.; and retained sects. *Cervicina* A. DC., *Lobelioides* A. DC., and *Linarioides* A. DC. Although the infrageneric classifications of the De Candolles generally have not been accepted in subsequent treatments and revisions (e.g., Von Brehmer, Lothian, Tuyn in Moeliono & Tuyn, Thulin), no formal alternative has been proposed.

Two species of *Wahlenbergia,* each a fairly recent introduction, are credited to the southeastern United States. Section AIKINIA (herbs, often annual, rarely subshrubs; the ovary 2- to 5-locular) of Australasia is represented by *W. marginata* (Thunb.) A. DC. (*W. gracilis* (Forster) A. DC.), $2n = 54$, 64, 72, and ca. 90. (Among recent workers, Carolin is seemingly alone in his opinion that *W. gracilis* is not conspecific with *W. marginata.*) A variable species throughout its wide natural range (China and Japan through southeastern continental Asia and Malaysia to Australia and New Zealand [Tuyn in Moeliono & Tuyn]), *W. marginata* was first collected in North America in Alachua County, Florida, in 1937 (see Ward; see, however, McVaugh, 1945a). Within a few years it was known in Florida from the central panhandle, as well as farther south in the peninsula. *Wahlenbergia marginata* is presently known from stations across the Gulf and Atlantic coastal plains from southern Louisiana to southern North Carolina. It seems to be mostly absent from more interior parts of the Coastal Plain, as well as from southern Florida. However, Shinners compared its spread

[11]Although *Lightfootia* is the oldest of the three generic names involved, it is a later homonym of *Lightfootia* Sw. (Flacourtiaceae) and therefore illegitimate. *Cephalostigma* was published in 1830.

[12]In Alphonse de Candolle's *Monographie des Campanulées,* which includes the protolog for this section, *Nesophila* heads the description and treatment of species (p. 160), but *Nesophyla* appears in the *Conspectus Generis* (p. 130).

through the Southeast to that of two other adventives from southeastern Asia, *Digitaria violascens* Link (Gramineae) and *Perilla frutescens* (L.) Britton (Labiatae) and presumed that it would eventually occupy much of the same range (i.e., most of our range, as well as more northern localities in the United States). *Wahlenbergia marginata* grows in sandy or gravelly substrates primarily along roadsides or railways and in sandy pine woods.

The monotypic sect. LINARIOIDES (perennial herbs, with 2-locular ovaries) of South America is represented in the Southeast by *Wahlenbergia linarioides* A. DC. Apparently first collected in North America in 1958 in westernmost Florida (Ward, Godfrey), the species has since been found across the northern portion of the state, but evidently not in the peninsular part. Although the flowers have been reported to be pale blue (vs. purplish blue in *W. marginata*), they are only rarely nonwhite, according to Burkhalter, who has observed the plants for over ten years at numerous places along roadsides and in sandy pine woods in the Pensacola, Florida, area. Compared to *W. marginata, W. linarioides* is much less common and widespread in the Southeast, has capsules that open by two (vs. three) apical valves, and has flatter seeds that are otherwise more isodiametric (i.e., nearly circular) (vs. elliptic) in face view. The differences in seed shape are easily discernible in most herbarium material.

Richardson noted a resemblance between plants of *Wahlenbergia linarioides* from Chile and species on the Juan Fernández Islands belonging to sect. NESOPHILA (in part characterized by two-locular capsules), which he considered to be polyphyletic and to demonstrate the convergence often associated with colonization of tropical and subtropical oceanic islands. Such observations are consistent with the notion that existing infrageneric classifications of *Wahlenbergia* seem in general to be unnatural.

The base chromosome number in *Wahlenbergia* is $x = 9$, according to Gadella (1966a), with diploids, tetraploids, hexaploids, and octaploids (i.e., $2n = 18$, 36, 54, and 72) having been reported (see Bolkhovskikh *et al.*). As indicated above, *W. marginata* demonstrates a high level of infraspecific cytological and morphological variation. The report of $2n = 32$ in two species of *Edraiantha* (see Gadella, 1966b) is consistent with the segregation of this group from *Wahlenbergia* (see A. P. de Candolle), although, for example, $2n = 64$ has been reported for *W. marginata* (Sugiura).

Anatomical features of *Wahlenbergia* include a variously developed leaf hypodermis (as in xerophytic species of South Africa); a clearly defined stem endodermis, sometimes with Casparian thickenings; and medullary bundles in the stem (of some species). The wood of the Campanulaceae has been described largely from observations involving species of *Wahlenbergia* (Metcalfe & Chalk, 1950).

The pollen is binucleate when shed in the extraregional *Wahlenbergia bicolor* Lothian (Davis) and trinucleate in *W. marginata* (Subramanyam, 1948). The grains of *W. marginata* are reportedly spheroidal, tetraporate (the pores on slightly elevated parts of the exine), and reticulate, with an outermost layer of microechinate ornamentation (Subramanyam, 1948; see also Dunbar, 1975a, *fig. 12,* for SEMs of other species). Pollen of *W. bicolor* has three pores (Want).

The embryology of *Wahlenbergia* conforms in general to that of the Cam-

panulaceae as a whole (see Subramanyam, 1948), although several features are notable and perhaps unique in the genus. Subramanyam (1948) studied ovule and seed development in *W. marginata* and found that in rare cases it is the third megaspore (instead of the usual fourth) that enlarges, a feature that has also been recorded in *Lobelia trialata* Buch.-Ham. (see Subramanyam, 1948). The synergids are long and show characteristic hooklike projections that have also been observed in *Pentaphragma* (Davis), and although antipodal degeneration is usually in accord with that seen throughout the Campanulaceae, it appears to occur slightly earlier in *Wahlenbergia* (Subramanyam, 1948). Rosén (1932, 1949), who identified in the Campanulaceae three types of endosperm formation (viz. Codonopsis, Phyteuma, Sphenoclea types—see family discussion) that appear to cross taxonomic lines, listed *Wahlenbergia* among genera with the Codonopsis type. Transverse walls are first formed in the chalazal cells in *W. marginata* (Subramanyam, 1948) and *W. bicolor* (Want), but according to Rosén (1949) such divisions usually take place among micropylar cells in the endosperm of Campanulaceae in general. Polyembryony has been reported in *W. gracilis* (Subramanyam, 1947).

Autogamy is the rule in *Wahlenbergia marginata* (Docters van Leeuwen in Moeliono & Tuyn) and may also occur in other species of the genus, even though the stigma opens long after pollen release (Tuyn in Moeliono & Tuyn). Haviland stated that the anthers dehisce introrsely before the opening of the bud, so that the style becomes coated with pollen (glands on the style secrete a glutinous fluid). Cross pollination may be effected when this pollen is subsequently removed by insects (apparently chiefly bees). According to Lothian (1947a), autogamy may also result if the recurving stigmatic lobes encounter pollen when finally contacting the style.

Lothian (1947a) concluded that Australian species of *Wahlenbergia* rarely hybridize in nature, even though this process had been invoked to explain much of the considerable variation observed in the genus. Experimental work by Lothian (1947a) indicated that although several vegetative parts were susceptible to modification by the environment, floral parts were essentially unchanged.

Although propagation is usually by seed, vegetative reproduction by means of stolons, suckers, and pieces of detached root occurs in *Wahlenbergia* (Lothian, 1947a).

According to Muller, Mildenhall's report that in New Zealand *Wahlenbergia* pollen first appeared in the mid-Pliocene is undocumented.

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4. **Jasione** Linnaeus, Sp. Pl. **2:** 928. 1753; Gen. Pl. ed. 5. 400. 1754.

Erect, ascending, or spreading, terrestrial, biennial (sometimes perennial or annual) herbs. Stems either unbranched or less branched above than near the base, less leafy (or leafless) above than below and often with short, leafy, axillary branches. Leaves alternate, sessile; blade linear-oblong to linear-lanceolate, the apex obtuse or subacute, the margin undulate, entire or remotely and shallowly crenate, ciliate. Inflorescence a terminal globose umbel; flower maturation centripetal; involucral bracts numerous, shorter than the flowers, triangular-acute to ovate-cuspidate, entire, crenate, or serrate; peduncles long, leafless except near the base. Flowers small, numerous, pedicellate, perfect. Calyx actinomorphic; tube ovoid or turbinate; lobes 5, subulate, erect. Corolla actinomorphic; lobes 5, linear, erect to spreading, exceeding the calyx lobes. Stamens 5, free from the corolla; filaments subulate; anthers usually coherent but only at the base (less so to free in bud). Ovary inferior, locules 2; placentation axile; stigma lobes 2. Fruit an ovoid to turbinate capsule, dehiscent by 2 apical pores; seeds amber colored, often much darker at the ends, oblong, lustrous. (Including *Jasionella* Stoianov & Stefanov.) TYPE SPECIES: *J. montana* L. (*Jasione* listed by Linnaeus, Critica Botanica, p. 104. 1737 [p. 84 in English transl. by A. Hort, 1938], as a Greek name provided by Theophrastus; name derived from Greek *iásis,* healing.)—SHEEP'S-BIT.

A small, essentially European genus most obviously differing from other southeastern Campanulaceae in its umbellate, involucrate inflorescence. Although Linnaeus recognized only *Jasione montana* L. in the first edition of his *Species Plantarum,* nearly a hundred species names have been published since. As it is presently understood, however, the genus includes only 5–15 species, most of which were placed by Kovanda in four informal groups (neither described nor named, although four representative species were indicated). Schmeja (cited in Kovanda), on the other hand, reportedly recognized 13 species in two subgenera.

Jasione has most commonly been allied at the tribal or subtribal level with (among southeastern genera) *Platycodon, Wahlenbergia,* and (less frequently) *Campanula* (A. de Candolle, A. P. de Candolle, Bentham & Hooker, Baillon, Schönland). In the system of Fedorov, *Jasione* was placed in the monogeneric Jasioneae Fedorov, one of eight tribes comprising the Campanuloideae. *Jasione* is included here with *Wahlenbergia* in the tribe Wahlenbergieae.

Jasione is represented in the New World and in the Southeast by *J. montana,*

a native of Europe and the Mediterranean region (including parts of northern Africa). Although widely distributed in its native range (to as far as 62° N latitude, and from low elevations more sporadically to the subalpine and alpine zones), the species appears to be most abundant in areas with an oceanic climate. It is best adapted to full sun and well-drained soils (Bailey *et al.*) and is therefore most frequent on sandy soils in pine woods, stabilized dunes, heaths, and dry, grassy places (Kovanda). Of several infraspecific taxa that have been described in this variable species, only two appear to be tenable. Varietas *montana* is a diploid, $2n = 12$, and a strict calcifuge, while var. *litoralis* Fries, $2n = 14$ (an aneuploid), is known only from saline soils in northern Europe; the typical variety is unknown from such habitats (Kovanda; see Tutin regarding var. *littoralis* Boiss., evidently a different taxon).

In North America *Jasione montana* has become established mostly along the east coast from Massachusetts to North Carolina, where it demonstrates the same climatic and ecological affinities prevalent in Old World populations of var. *montana.* Although the species was established and spreading on Long Island by 1925 (Burnham & Latham), it seems to have remained unknown in the Southeast until more recently. It was not included for this region by Small (1933) but was listed about 30 years later by Radford *et al.* as a roadside rarity from Moore Co., North Carolina.

The base chromosome number in *Jasione* appears to be $x = 6$ (Kovanda). Although diploids, tetraploids, hexaploids, and decaploids (i.e., $2n = 12$, 24, 36, and 60) have been reported, polyploids are evidently unknown in *J. montana.* Parnell (1982a) found a relatively low recombination index (number of haploid chromosomes plus average number of chiasmata per meiotic cell) and a high percentage of terminal chiasmata in *J. montana,* each considered an alternative to self fertilization (see discussion of breeding biology, below) as a means of bringing about a temporary reduction in the level of genetic recombination.

According to Parnell (1982b), Poddubnaya-Arnoldi showed that the pollen of *Jasione montana* is binucleate. Dunbar (1973b) found it to be similar to that of *Campanula* in shape (spheroidal) and aperture type and number (3 or 4 pores), but different in that the basal divisions of the spinules are less pronounced, the sculptured elements are in a more irregular pattern, the pores lack opercula, and the tectum is perforated. Pollen inviability was shown to vary within inflorescences, among flowers maturing at different times, and within populations of *J. montana.* Plants with very high percentages of inviable pollen (up to 99 percent), as well as completely male-sterile plants, are evidently sporadically distributed throughout the range of the species (Parnell, 1982b).

The ovule of *Jasione montana* in general conforms to that characteristic of the Campanulaceae (see Berger & Erdelska; Erdelska, 1968), except that the integument is so transparent that it is possible to study the living embryo sac (Erdelska, 1968). While the megagametophyte is generally of the Polygonum type, the position of the egg cell is possibly unique among angiosperms in that it usually appears to be separated from the embryo sac wall by the synergids (Berger & Erdelska). Embryogeny appears to be of the Solanad type (see Souèges).

The breeding biology of *Jasione montana* was studied in detail by Parnell

(1982b). Pollen is released onto the hairy, brushlike distal half of the style well before the flower opens. Elongation at the stylar base causes the emergence of this pollen, most of which is removed by insects within a few days. The two stigmatic lobes diverge after about a week, but never reflex enough to come into contact with the style or any of what little pollen might remain on it by this time. Experiments indicated that neither cleistogamy nor agamospermy is an effective means of reproduction in the species (although each may occur), and that the temporal and spatial separation of released pollen and receptive stigma (combined with the early removal of pollen by insects) is very effective in preventing self pollination in nature. Experiments also suggested that, in general, geitonogamy (fertilization between flowers of the same individual) is more effective than autogamy—but less successful than allogamy—under natural conditions. Most insects crawl from one flower to another in each umbel as well as from one umbel to another during a visit to any one plant. Since the flowers encountered are therefore in various stages of development (the outermost in each inflorescence being the most advanced), geitonogamy could be effected.

Jasione montana is the most wide ranging and variable species in the genus. Browsing by animals causes an increase in branching, reduction in umbel size, and change in involucral-bract shape, although genetic and ontogenetic factors also appear to be involved (Pugsley). In addition, there is considerable variation in the degree of pubescence of most above-ground parts, as well as in the color of the corolla. It is unlikely that polyploidy contributes to polymorphism in this species (see above). Environmental modification and genetic recombination are instead the more likely causes (Kovanda).

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Subfam. LOBELIOIDEAE Schönland, Nat. Pflanzenfam. IV. **5**: 63. 1889.

5. **Lobelia** Linnaeus, Sp. Pl. **2**: 929. 1753; Gen. Pl. ed. 5. 401. 1754.

Erect, ascending, or decumbent, terrestrial to aquatic, annual, biennial, or perennial herbs [or shrubs]. Leaves alternate, sessile to short petiolate, variously serrate, crenate, or subentire (often within the same species). Inflorescence a terminal, often loose, bracteate (bracts often leafy) spike, raceme, or panicle. Flowers resupinate [rarely not] at anthesis, perfect [rarely staminate or carpellate, and the plants then dioecious]. Calyx more or less actinomorphic, the tube mostly ribbed and hemispheric; lobes 5, much longer than the tube, entire or often glandular toothed, sometimes with basal appendages. Corolla mostly united below, zygomorphic and bilabiate, the tube usually with an adaxial (after resupination) fissure extending from its apex nearly to its base, through which the stamens and enclosed style and stigma are more or less exserted; the upper (after resupination) lip 2-lobed, the lower 3-lobed. Stamens 5, free from the corolla; filaments connate except at the base; anthers basifixed, connate in a ring around the style, usually the lower 2 shorter and tufted and the upper 3 longer and with incurved tips that partially occlude the anther tube. Ovary half inferior to inferior, 2-locular; placentation axile; style enclosed by the staminal tube; stigma lobes 2, expanding after protrusion beyond anther tube. Fruit a hemispheric capsule with marcescent corolla, stamens, and style/stigma, dehiscent by apical, loculicidal pores [to more berrylike]; seeds yellowish brown, tuberculate, oblong. (Not *Lobelia* Miller, 1754, = *Scaevola* L., 1753, nom. cons.) LECTOTYPE SPECIES: *L. Dortmanna* L.; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **3**: 299. 1913. (*L. cardinalis* L. was selected by M. L. Green in Hitchcock & Green, Prop. Brit. Bot. 184. 1929; a type not designated, according to *Index Nominum Genericorum* **2**: 997. 1979.) (Named for Matthias de l'Obel, 1538–1616, Flemish botanist and herbalist.)

A cosmopolitan genus comprising at least 365 species, according to Wimmer, the most recent monographer of the group on a worldwide basis. A clear majority of the species are native to Australia and Africa, although large numbers are indigenous to Mexico, Central and South America, and various Pacific Islands. Several species occur in China and eastern Asia, but only two are native to western Europe. It is the widest-ranging genus within the Lobelioideae (Wimmer) and is the only one with members in our area. Of the 25–30 species

FIGURE 2. **Lobelia.** a–l, *L. cardinalis:* a, tip of flowering stem, × ½; b, flower with fenestration (in black) behind nearest calyx lobe at base of corolla, staminal tube with enclosed style and undeveloped stigma exserted through fissure between 2 upper corolla lobes, × 2; c, flower with corolla removed, filaments monadelphous except at base, stigmas just beginning to expand, × 2; d, anther tube formed by connation, the lower 2 anthers shorter and tufted, × 4; e, cross section of anther tube after dehiscence, style in center, × 6; f, tip of style with stylar brush and unexpanded stigmas at time of anther

present in North America, all but a few are confined mostly to the area east of the Mississippi River.

In the Southeast species of *Lobelia* are easily distinguished from other Campanulaceae by characters that separate the two major subfamilies (e.g., they have zygomorphic corollas, connate anthers and upper filaments, and two carpels; see family discussion). The genus was placed by Wimmer in the Lobelieae (top of ovary conical instead of flat, fruit usually dehiscent instead of indehiscent), one of two tribes recognized in his treatment of the Lobelioideae. *Lobelia* is further distinguished within the tribe by a combination of characters that include a slit between the two adaxial (after resupination) lobes of the corolla, the exsertion through this slit of stamens and enclosed style and stigma, and a subglobose to elliptic, pedicellate, bilocular capsule with axile placentation and apical, loculicidal dehiscence.

Lobelia is perhaps most closely allied to *Pratia* Gaudich., of the Southern Hemisphere, even though the latter was placed by Wimmer in the Delisseeae Reichenb. (top of ovary flat, fruit indehiscent). Although *Lobelia* and *Pratia* are indistinguishable by floral characters, they were until recently generally accepted as distinct on the basis of fruit type, which in *Pratia* is often a vividly colored berry. Moeliono & Tuyn have reported, however, that although Asiatic and western Malaysian individuals of *Pratia angulata* (Forster f.) Hooker f. (*Lobelia angulata* Hooker f.) produced such fruit, the pericarp in eastern Malaysian material was drier and thinner (almost membranaceous), and the apex became convex and even tardily dehiscent (by two valves). In one case they reported fleshy, indehiscent berries and true capsules in the same collection. Adams indicated that in the West Indies these genera are not separate; Mabberly (1975a) considered them closely allied; and Ydrac showed that they are indistinguishable in vegetative anatomy. Because such observations suggest that the tribes of Lobelioideae proposed by Wimmer are unnatural, they are not recognized here.

The species of *Lobelia* occurring in the southeastern United States were placed by McVaugh (1943) in two of six sections recognized for North American plants (no other infrageneric taxa were designated). Wimmer, on the other hand, placed all of our species in sect. *Hemipogon* Bentham (= sect. LOBELIA), one of two sections comprising subg. *Lagotis* E. Wimmer (= subg. LOBELIA). Section *Hemipogon* was further divided into two subsections. One (or perhaps two) of our species (*L. homophylla* E. Wimmer; *L. Cliffortiana* L. actually may not occur in our area) was placed in subsect. *Leiospermae* E. Wimmer, while the remainder were assigned to subsect. *Trachyspermae* E. Wimmer (= subsect.

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dehiscence, × 12; g, expanded stigmas protruding from anther tube, × 4; h, expanded stigmas, × 12; i, diagrammatic cross section of ovary with 2 locules, each nearly filled by an axile placenta and numerous ovules, × 6; j, diagrammatic longitudinal section through half-inferior ovary with numerous ovules and axile placentation, × 3; k, capsule after dehiscence, with persistent calyx, corolla, stamens, and style/stigma, × 3; l, seed, × 25. m, flower of *L. siphilitica,* staminal tube with enclosed style and undeveloped stigma partly exserted through fissure between 2 upper corolla lobes, × 2.

Lobelia). Subsection *Trachyspermae* was divided into two "greges," one of which, grex *Cardinales,* included one of our species (*L. cardinalis* L.), and the other of which, grex *Coelestes* (= grex *Lobelia*), contained the others and was divided into two "subgreges." Subgrex *Dortmanna* (= subgrex *Lobelia*) included the extraregional *L. Dortmanna* L., and subgrex *Kalmia* included the remainder of our species (perhaps 18), forming what could be called a primarily southeastern (United States) assemblage. The relatedness of these approximately 18 species was also recognized by McVaugh (1943), who included them, together with *L. cardinalis,* in sect. *Dortmanna* (= sect. LOBELIA).

From consideration of data including those provided by cytogenetics, Bowden (1959b) recognized four major (but unnamed) lines of evolution among North American species of subsect. *Lobelia* sensu E. Wimmer. In three of these lines, only a single, diploid species remains extant. These are *L. inflata* L. and the extraregional *L. Dortmanna* and *L. Kalmii* L. According to Bowden (1959a), the three do not hybridize either with each other or with any other North American species of *Lobelia.* The fourth major line included three subordinate lines: a group with small (7–15 mm) flowers, one with small to medium (11–33 mm) flowers (and narrow leaves), and a third with medium to large (15–50 mm) flowers.

Primarily for purposes of presentation, I have for the most part followed the infrageneric classification of Wimmer, with Bowden's divisions applied to subgrex *Kalmia* (i.e., all of our species except *L. homophylla, L. cardinalis,* and perhaps *L. Cliffortiana*). In general, the species concepts of McVaugh (1943) appear to be sound and are employed here.

Subgenus LOBELIA is characterized by distinctly bilabiate corollas (vs. less distinctly bilabiate or unilabiate corollas in subg. MEZLERIA (Presl) E. Wimmer and subg. TUPA (G. Don) E. Wimmer) that have two more or less erect adaxial lobes. The distribution of the subgenus is largely that of the genus as a whole, with the exception that it does not appear to be as well represented in tropical Africa or on islands in the Pacific Ocean. Section LOBELIA (all of our species) includes plants in which the two shorter, adaxial (lower) anthers are pilose-penicillate apically (vs. all anthers equal in length and pubescence in sect. HOLOPOGON Bentham). The pubescence characters of the anthers were not considered by McVaugh (1936) to be of taxonomic value.

Species of subsect. *Leiospermae* have seeds with smooth surfaces. *Lobelia homophylla* is an annual plant with ovate, often crenate (or dentate to serrate) leaves that are cauline but sometimes clustered near the base; basal bracteoles; entire calyx lobes; blue, nonfenestrate corollas; mature capsules that are one-third or less inferior; and ellipsoid seeds. The species occurs in pinelands and along fence-rows and roadsides and is known only from peninsular Florida. *Lobelia Cliffortiana,* $2n = 14$, is very similar to *L. homophylla* but differs in its sometimes lanceolate or elliptic upper leaves, usually larger flowers, and more-than-half-inferior capsules. *Lobelia Cliffortiana* has been reported to occur as a weed in wet places, waste places, and cultivated ground on the Coastal Plain from Florida to Texas (Small, 1933). McVaugh (1940b, 1943) reported that, although it is native to the Greater Antilles, it has been introduced in Trinidad and various tropical and subtropical mainland areas in the New

World, as well as in the Old World tropics. Ward stated that the species has been incorrectly attributed to Florida, evidently through confusion with *L. homophylla*. I have seen no smooth-seeded specimens from the Southeast that do not belong to *L. homophylla*.

Subsection *Lobelia* is characterized by seeds that are markedly roughened. This feature distinguishes all native North American species of *Lobelia* (with the exception of *L. homophylla*) from those of other parts of the world and (according to McVaugh, 1936) indicates a common ancestry for them. Grex *Cardinales* is a North American group of about four species that differ in flower color from grex *Lobelia,* a North American and northern European assemblage (of which only *L. Dortmanna* occurs outside of North America). With the exception of occasional white-flowered plants in both groups, members of grex *Cardinales* have red (vs. blue) corollas. (Such a distinction may be unnatural: some species of grex *Lobelia* [e.g., *L. inflata, L. floridana* Chapman] may have pink flowers; and *L. cardinalis* [grex *Cardinales*] may be most closely related to *L. siphilitica* L. [grex *Lobelia*].)

Grex *Cardinales* is represented in the Southeast by *Lobelia cardinalis,* $2n = 14$, a familiar and attractive plant that grows in wet ravines and swamps and along lake shores and streambanks throughout our range. Although McVaugh (1952) considered this species to be most closely related to the northern *L. rotundifolia* Juss. ex A. DC. (but to have evolved somewhere south of central Mexico), Bowden (1959b) hypothesized, in part on the basis of cytogenetic evidence, that *L. cardinalis* is more closely related to *L. siphilitica* and that it evolved in the Southeast. Bowden further proposed that the two commonly recognized subspecies of *L. cardinalis* were derived from ancestral populations in our area. While subsp. *cardinalis* (leaves lanceolate to ovate-lanceolate, blades mostly 3–5 times as long as wide) spread farther north to Minnesota and New Brunswick and west to Texas, subsp. *graminea* (Lam.) McVaugh (leaves linear to ovate-lanceolate, blades mostly 6–12 times as long as wide) migrated along the Gulf of Mexico through Texas and Mexico to as far south as Panama, with a number of varieties evolving in the process. Bowden therefore considered subsp. *graminea* (which does not occur in the Southeast) to have migrated secondarily to the Southwest from Mexico and farther south, whereas McVaugh contended that this migration was a primary one.

Grex *Lobelia* was divided by Wimmer into two subgreges. Subgrex *Lobelia* (leaves linear, bitubulate) is monotypic, including only *L. Dortmanna,* of northern North America and northwestern Europe, while subgrex *Kalmia* (leaves variously shaped, flat), with the exception of *L. Kalmii* L., of northern North America, comprises species that are native to and/or endemic in the Southeast.

Lobelia inflata, $2n = 14, 16$, although small flowered, is somewhat removed from the other small-flowered species in subgrex *Kalmia* (Bowden, 1959a, 1959b). It is superficially reminiscent of *L. Cliffortiana* but has roughened seeds, as well as inflated capsules. It is recognizable in flower by its narrow, entire calyx lobes that often exceed the corolla in length, as well as by the presence of leafy floral bracts in the lower portion of each inflorescence. It differs from *L. spicata* Lam., another small-flowered species with which it is sometimes confused, by its quickly maturing capsules that render the flowering

portion of the inflorescence relatively short. Krochmal and colleagues (1972a) stated that the corollas of *L. inflata* are violet to pinkish white. The species probably originally inhabited dry places in open woods, but has since spread to dry roadsides and waste places. Laboratory work has shown that plants are adversely affected when the soil pH is greater than seven (Krochmal & Magee). *Lobelia inflata* occurs throughout the eastern United States, with fewer localities west of the Mississippi River. In the Southeast it is more common in the northern tier of states and appears to be quite rare on the Coastal Plain.

Lobelia spicata Lam., $2n = 14$, and six other small-flowered southeastern species comprise the first of Bowden's three subordinate lines within his fourth major line in subsect. *Lobelia* sensu E. Wimmer (see above). *Lobelia spicata, L. appendiculata* A. DC., and *L. Gattingeri* Gray differ from the other four small-flowered species in their relatively short pedicels that give the inflorescence a spikelike appearance. The three seem to be closely related and intergrade in a number of morphological features, including the pubescence characters by which they are, nevertheless, most easily separated. The calyx lobes are glabrous (or nearly so) in *L. spicata,* glabrous in *L. Gattingeri,* and pubescent in *L. appendiculata*; the bases of the stems in *L. spicata* are for the most part conspicuously pubescent, while those of *L. Gattingeri* are glabrous or sometimes have a few chaffy hairs. *Lobelia spicata* differs from all other small-flowered species in its more congested inflorescences that taper more gradually toward the apex. *Lobelia spicata* occurs throughout most of the area from southeastern Saskatchewan to eastern Texas and New Brunswick; in the Southeast it does not seem to occur on the Coastal Plain southeast of a line from about New Orleans to northeasternmost North Carolina. The plants grow in moist or dry places in woods, fields, and meadows. Several varieties of *L. spicata,* supposedly differing in leaf arrangement, pubescence, and calyx appendages, have been named and are represented in the Southeast but are reportedly connected by intermediates (McVaugh, 1943).

In addition to differences in inflorescences, *Lobelia appendiculata* and *L. Gattingeri,* $2n = 14$, differ from *L. spicata* in their thinner, smoother, sessile cauline leaves that are rounded at the base (vs. tapered to a petiole in *L. spicata*). The two species are closely related and, according to McVaugh (1943), nearly indistinguishable by vegetative characters. Although McVaugh (1936) initially maintained them as distinct species because of the very restricted range of *L. Gattingeri* (see below) and an apparent lack of intermediates, he clearly indicated that such a position was only tentative and later, with no further discussion (1943), treated them as conspecific varieties (*L. appendiculata* var. *appendiculata* and var. *Gattingeri* (Gray) McVaugh). Bowden (1959a, 1959b), however, considered the two entities to be specifically distinct on the basis of a combination of traits including, in *L. Gattingeri,* shorter stems, glabrous (vs. ciliate) calyx lobes, and a lack of auricles, even though McVaugh (1936) had indicated that both the ciliation of the calyx lobes and the length of the auricles were very variable in *L. appendiculata.* It is clear that the situation deserves further attention.

Lobelia appendiculata grows in moist to dry sandy soils in pinelands, open woods, and prairies in central Alabama, Louisiana, and the southwestern half

of Arkansas, as well as in eastern Texas, southern Oklahoma, and eastern Kansas. *Lobelia Gattingeri* is known only from a small area in the limestone region of central Tennessee in seeping or springy places on calcareous bluffs and in cedar barrens (see Baskin & Baskin).

The four remaining small-flowered species generally have longer pedicels and thus more racemelike inflorescences than the foregoing three. *Lobelia Boykinii* Torrey & Gray and *L. Canbyi* Gray, both $2n = 14$, have linear, sessile, cauline leaves and lack the broader basal leaves seen in *L. Feayana* Gray and (often) in *L. Nuttallii* Roemer & Schultes. *Lobelia Boykinii* is a more delicate plant than *L. Canbyi,* with shorter, narrower leaves (not more than 0.5 mm wide). *Lobelia Boykinii* also lacks bracteoles on the pedicel, and it flowers in the spring or early summer; *L. Canbyi* has a pair of bracteoles near the base of the pedicel, and it flowers from July to October. *Lobelia Boykinii,* the only rhizomatous species of *Lobelia* in our area (Godfrey & Wooten), is an often-immersed plant of pineland swamps or cypress ponds (also savannas, see Bowden [1959a] and Radford *et al.*) on the Coastal Plain in northern Florida, Georgia, and the Carolinas, northward to southern Delaware (McVaugh, 1936). *Lobelia Canbyi* usually grows in pineland swamps and savannas in parts of Tennessee, Georgia, and the Carolinas and is evidently confined to pine barrens in Delaware and New Jersey. McVaugh (1936) considered *L. Boykinii* to be a distinct, Coastal Plain species of obscure affinities and (evidently) superficial resemblance to *L. Canbyi.*

Lobelia Nuttallii, $2n = 14, 28$, may closely resemble *L. Canbyi* (plants of each species have linear cauline leaves and a pair of basal bracteoles on the pedicels), especially when the broad basal leaves are absent. (The rosette leaves in this species, and apparently in others including *L. flaccidifolia* and *L. appendiculata,* are sometimes shed prior to anthesis; the persistence of these leaves in *L. spicata* is evidently under a greater degree of genetic control [Godfrey & Wooten].) However, *L. Nuttallii* is a more slender plant (at the base the stem is usually 0.5–1 mm wide, vs. 1.5–3.5 mm), with pedicels that are glabrous or nearly so (vs. densely pubescent) and in length usually greater than or equal to (vs. less than or equal to) the subtending bract. *Lobelia Nuttallii* is frequent among wiregrasses (*Aristida stricta* Michaux) in moist pinelands and savannas, sometimes in brackish marshes or dry places and usually in acid conditions. It occurs from central Tennessee and adjacent Kentucky to Louisiana, Alabama, and northern Florida and northward to Long Island, New York. Brooks & Hauser considered it a probable introduction in southeastern Louisiana.

Lobelia Feayana, $2n = 14$, is smaller and less erect than *L. Nuttallii,* although the two are otherwise quite similar morphologically. The lower stems are usually trailing, uniquely (among our species) rooting at the nodes and sometimes mat forming (Godfrey & Wooten); only the flowering stems are ascending. Although it has rosette leaves similar to those often seen in *L. Nuttallii,* they are often broadly ovate to suborbicular (vs. usually spatulate) and grade (instead of abruptly change) into the cauline leaves, which become narrower toward the apex of the plant (but which are generally neither as narrow nor as numerous as those in *L. Nuttallii*). *Lobelia Feayana* also has more elongate capsules that are two-thirds or more (vs. one-half) inferior. It occurs in moist and/or sandy

places, seashores, swamps, and pinelands, and it is endemic to peninsular Florida (though evidently absent from the southernmost portions of that state, viz., Monroe and Dade counties). *Lobelia Nuttallii* was thought by McVaugh (1936) to have given rise to *L. Feayana* in northern Florida, where the two species now intergrade to some extent.

Four species with mostly narrow leaves and small to medium flowers comprise the second of Bowden's subordinate lines of evolution within his fourth major line in subsect. *Lobelia* sensu E. Wimmer. *Lobelia floridana* and *L. paludosa* Nutt., both hexaploids ($2n = 42$), have large basal leaves and much smaller, less numerous cauline leaves. The species are morphologically close and often indistinguishable by vegetative characters except that *L. floridana* is usually a larger plant. *Lobelia floridana* is most readily distinguished from *L. paludosa* by its almost always nonfenestrate corollas and its longer (at least 3 mm) filament tubes. *Lobelia floridana,* which according to Bowden (1964b) has pink corollas, occurs in moist pinelands and on the borders of ponds in pinelands and cypress swamps. Its distribution overlaps that of *L. paludosa* only in the area of the Apalachicola River in northwestern Florida, and from there it extends along the Gulf Coast to southwestern Louisiana. It is also known from an isolated area in southeastern (coastal) North Carolina. *Lobelia paludosa* is often emergent, growing in low areas in pinelands, as well as in ponds, in southeastern Georgia and all but westernmost Florida.

Two other narrow-leaved species have only cauline leaves, of which the lower ones are usually larger. Both have sessile upper leaves, but the lower leaves are short-petiolate in *Lobelia flaccidifolia* Small (*L. Halei* Small), $2n = 14$, and usually sessile in *L. glandulosa* Walter, $2n = 28$. Compared to *L. glandulosa, L. flaccidifolia* has flowers that are more numerous and in tighter, less secund racemes (a difference that persists in fruit). In addition, *L. glandulosa* has fenestrate corollas. Both are Coastal Plain species: *L. flaccidifolia* occurs in river swamps from southeastern Georgia to the northern Gulf Coast of Texas, and *L. glandulosa* grows in swamps and wet places, often in pinelands, from Florida to southern Virginia and perhaps from more isolated localities in Mississippi and Texas.

Six species of *Lobelia* occurring in our area have medium to large flowers and constitute the last of Bowden's three subordinate lines of evolution. *Lobelia amoena* Michaux and *L. elongata* Small, both $2n = 28$, have upright, unbranched, and relatively coarse stems. Bowden (1960a) proposed that each species is of hybrid origin, involving diploid plants that were probably ancestral to *L. puberula* Michaux (see below) as one of the parental species. *Lobelia amoena* differs from *L. elongata* in its elliptic to ovate, rarely lanceolate leaves that are 1.5–4.5 cm broad (vs. narrowly elliptic and usually 1.5 cm or less wide) and its shorter filament tubes (8 mm or less vs. 8–11 mm long). (See McVaugh regarding the identity of these two species and the corresponding type material.) Two varieties, both of which are plants of swamps and moist woods in mountain and piedmont districts, are generally recognized in *Lobelia amoena.* Varietas *amoena* has entire (vs. toothed) calyx lobes and shorter filament tubes; it generally occurs in the western parts of the Carolinas, eastern Tennessee, northern Georgia, and eastern Alabama. Varietas *glandulifera* Gray (*L. geor-*

giana McVaugh) also occurs in this region but extends onto the Coastal Plain as well, into parts of western Florida and adjacent areas and eastern North Carolina and Virginia. A plant of tidal marshes but also occurring in swamps and on low ground near the coast, *L. elongata* is known from the area between Georgia and Delaware.

Four medium- to large-flowered species are diploids ($2n = 14$). *Lobelia brevifolia* Nutt. ex A. DC. (leaves numerous, short, sessile, divaricate to slightly ascending, short pectinate) and *L. puberula*[13] (usually with relatively dense stem pubescence) were thought by Bowden (1959b) to have been segregated relatively early in the history of the genus in the southeastern United States. Nevertheless, a close relationship is indicated by the frequency with which they hybridize (Bowden, 1961b; McVaugh, 1936; Ward). Individuals of both species usually have rather weak, unbranched stems, but the calyx auricles of *L. brevifolia* are broad and foliose and usually cover the calyx tube completely, while those of *L. puberula* are generally much smaller. Holroyd stated that the presence of medullary bundles in the stem is probably diagnostic for *L. puberula*, although this feature is apparently rare or unreported for the Lobelioideae in general (Metcalfe & Chalk, 1950). Bowden (1960a) discovered a haploid seedling among the progeny of one of his experimental crosses, indicating a low frequency of parthenogenesis in *L. puberula*.

Lobelia puberula occurs in wet places and various kinds of soils in woods, on low ground, and in thickets throughout most of the southeastern United States and adjacent areas. Turner reported it from a "bog" in eastern Texas, intermingled with what he considered the strikingly dissimilar, though closely related, *L. Reverchonii* Turner, a species that enters our range in Louisiana (Rapides Parish). It differs from *L. puberula* in having greater distances between lower flowers (2.5–5 cm), densely hirsute pedicels and calyx bases, recurved lower corolla lobes, and longer corollas (9–15 mm) and anther tubes (4–6 mm). *Lobelia brevifolia* usually grows on damp, sandy soils in pinelands and is restricted to the Coastal Plain from the Florida panhandle to eastern Louisiana, usually near the coast. McVaugh (1936) indicated that on the basis of flower structure this species is related to *L. glandulosa*.

Lobelia siphilitica, $2n = 14$, and *L. cardinalis*, the other two diploid species in Bowden's medium- to large-flowered line, generally produce larger flowers than do any other species of *Lobelia* in the Southeast. Although strong morphological characters separate them, plants of each species are perennials and may be unique among southeastern members of *Lobelia* in that they form offset shoots (see, however, Holroyd, who stated that *L. inflata* and others also demonstrate this type of vegetative reproduction). Bowden considered each to be relatively recently evolved and to have shared a common ancestor with no other extant species. Artificial hybrids between the two are well known (e.g., Ames, 1903; Bowden, 1961a, 1964a, 1964b), but natural hybrids are evidently quite rare, though rather frequently reported (Bowden, 1964a; Ferreniea;

[13]McVaugh (1936) pointed out that the absence of type material makes the exact identity of *L. puberula* and its several morphologic/geographic phases impossible to determine, although later workers (e.g., Bowden, 1960a; Ward) have not reported such a problem.

McVaugh, 1943; Schneck; Steyermark; Witherspoon). Braun reported that they coexisted in the same garden for many years without hybridizing. It seems clear that reproductive isolation between these two species results from the fact that they do not normally share pollinators. Bees usually pollinate flowers of *L. siphilitica,* and although they may obtain nectar from *L. cardinalis* through the fenestrations in the base of the corolla (FIGURE 2b), they need not (and usually do not) contact pollen or stigmas in doing so (Robertson). Pollination in *L. cardinalis* is effected because hummingbirds or long-tongued lepidopterans contact pollen or receptive stigmas while obtaining nectar, which they accomplish by inserting their beaks or tongues into corolla tubes that are too narrow and too long for bees and the tongues of bees, respectively (Trelease). Wood (pers. comm.) observed plants of these species growing side by side at the Montreal Botanic Garden and reported that although some individual honey bees were actively collecting (blue) pollen from *L. siphilitica,* others were getting nectar through the fenestrations in the corollas of *L. cardinalis* without obtaining any of the (yellow) pollen of this species.

Lobelia siphilitica is a wide-ranging species in the United States east of a line from western North Dakota to western Texas, although it is poorly represented on the Coastal Plain in the Southeast. Two varieties are usually recognized. Plants of var. *ludoviciana* A. DC. are smaller and less hairy (to glabrous), with smaller leaves and flowers than those of var. *siphilitica.* They generally occur west of the Mississippi River, usually in wet places on prairies and in the mountains or on limestone cliffs, while individuals of var. *siphilitica* are generally found east of the Mississippi River in moist or wet, neutral to basic soils, often in light shade. Intermediates between the two varieties occur throughout the Mississippi Valley. *Lobelia cardinalis* differs most strikingly from all other species of the genus in our area in its red corollas, and on this basis it was considered by Wimmer to be unrelated to them.

A number of chemical studies have provided systematically relevant information concerning *Lobelia siphilitica* and *L. cardinalis.* Wilson investigated anthocyanin pigments from corollas; he found that a pelargonidin was present in *L. cardinalis,* and a delphinidin in *L. siphilitica* (see also Yoshitama). Gupta & Spenser provided evidence indicating that lobinaline, the major alkaloid in *L. cardinalis,* resulted from the dimerization of a monomer related to 8-phenyllobelol, a simpler alkaloid occurring in *L. inflata.* (*Lobelia inflata* contains all the known "lobelia alkaloids" except lobinaline [Keogh & O'Donovan].) Tschesche and colleagues (1964) suggested that two alkaloids isolated from *L. siphilitica* are chemically related to lobinaline. Bentley and coworkers reported that in *L. cardinalis* the aerial parts are richer in polyacetylenes than the roots, although the opposite is true of a hybrid with *L. siphilitica*; in both species and hybrid the major polyacetylene is enediynetriol.

The "lobelia alkaloids" are well known and are evidently restricted to the laticifers (Mascré & Crété). At least 14 different pyridine alkaloids have been isolated from *L. inflata* (Kingsbury), although most attention has been directed toward lobeline and related compounds because of their economic value. Flavonoids, triterpenes, and tannins, as well as other types of compounds, have also been detected in two extraregional species of *Lobelia* (Moreira).

Natural interspecific hybrids involving species of *Lobelia* are rare according to Bowden (1961a), with the exception of *L. brevifolia* × *L. puberula. Lobelia siphilitica* and *L. cardinalis* hybridize naturally, though rarely (see above), but Braun reported that *L. puberula* readily hybridized with *L. siphilitica* when plants of the two species were grown in the same garden. All five of these species are medium to large flowered, suggesting that such a grouping is indeed taxonomically sound.

Bowden (1961a, 1961b) reported the results of some 1400 attempted crosses involving 21 species of subsect. *Lobelia* (all but two of which occur in the Southeast) and 82 of a possible 420 species pairings. No hybrids involving *L. Dortmanna, L. Kalmii,* or *L. inflata* were obtained, supporting the notion that these species represent three distinct lines of evolution within grex *Lobelia.* However, Ames (1901) reported an artificially produced hybrid between *L. inflata* and *L. cardinalis,* and Simonet produced an artificial hybrid between *L. siphilitica* and *L. splendens* Willd. (of Mexico), which was placed in grex *Cardinales* by Wimmer. Such data, together with the affinities suggested above between *L. cardinalis* and other members of grex *Lobelia,* indicate that the segregation of grex *Cardinales* is unnatural.

The results of Bowden's attempted crosses support, to some extent, recognition of his three subordinate lines of evolution, except that this work indicated that the small-flowered group may be somewhat isolated from the other two (as, indeed, Bowden [1954] had earlier indicated). Hybrids were obtained from four pairs of species within the small-flowered group, from one pair within the narrow-leaved (small- to medium-flowered) group, and from nine pairs within the medium- to large-flowered group. Successful crosses were also made between groups, involving one pair of species from the small-flowered and the narrow-leaved groups, two pairs from the small-flowered and the medium- to large-flowered groups, and four pairs from the narrow-leaved and the medium- to large-flowered groups. In all, Bowden obtained hybrids between 21 pairs of species in subsect. *Lobelia,* all within his fourth major line of evolution, in which he put 18 species. In addition to these hybrids, twelve more, each involving the genomes of three to six species, were obtained. With the exception of the narow-leaved species *L. glandulosa,* which contributed to the formation of six of these hybrids, all of the species involved in these crosses were included in the medium- to large-flowered group.

Several anatomical features in *Lobelia* are worthy of note. An articulated, anastomosing latex system that is mainly confined to leaf and stem phloem probably occurs in most members of the Campanulaceae, but in plants of *Lobelia* it occasionally extends into the pith, and in two extraregional species into all parts of the flower as well (Metcalfe & Chalk, 1983). The general absence in the Lobelioideae of sclerenchyma in the pericycle of the stem and around the vascular bundles of the leaf is also notable (Metcalfe & Chalk, 1950), as is the presence of medullary bundles in the stems of *L. puberula* (Holroyd). Crystals of calcium oxalate have been reported in *L. inflata,* but Wallis demonstrated that such structures (in leaves) consist only of "fat."

Hewitt reviewed the literature pertaining to ovule and seed development in *Lobelia* and presented a detailed account of these and related topics (including

pollen) based on material of *L. amoena*[14] from the Carolinas. In general features of ovule and seed development, *Lobelia* conforms to the Campanulaceae as a whole, but there are some notable peculiarities. Cooper reported that in *L. cardinalis* the synergids and antipodals function as the chalazal and micropylar haustoria, respectively (*sic*; reversal of order probably inadvertent), instead of the usual condition (in angiosperms) in which the haustoria differentiate from cells of the endosperm (see, however, Subramanyam, 1952). However, Maheshwari determined that the synergids and antipodals in *L. trigona* Roxb. disintegrate at the time of fertilization, and that both kinds of haustoria develop from cells of the endosperm (see also Kausik, 1935; Kausik & Subramanyam, for *L. nicotianifolia* Heyne); Subramanyam (1951) later showed the same condition in *L. cardinalis.* Truly haustorial synergids probably only occur in a few species of Compositae (although detailed and illustrated accounts are lacking), according to Maheshwari, who also reported that the haustoria are formed from the endosperm in *Wahlenbergia gracilis* and *Sphenoclea zeylanica.*

Hewitt's account of ovule and seed development in *Lobelia amoena* is generally consistent with those provided for other species of *Lobelia,* including *L. nicotianifolia* (Kausik, 1938), *L. pyramidalis* Wallich (Subramanyam, 1949), *L. siphilitica* (Crété, 1938a), and *L. trigona* (Kausik, 1935). Polyembryony has been reported in *L. siphilitica* (Crété, 1938b).

Brewbaker reported that the pollen is binucleate when shed in five species of *Lobelia,* including *L. cardinalis,* and indicated that Schnarf's report of a trinucleate condition in the extraregional *L. nicotianifolia* needed to be verified. Nevertheless, trinucleate pollen was indicated for this species by Kausik (1938), for *L. cardinalis* by Cooper, and for the extraregional *L. pyramidalis* by Subramanyam (1949). Hewitt determined that the pollen of *L. amoena* is binucleate, although only fragments (if anything) remain of the tube nucleus at anthesis.

The pollen of *Lobelia cardinalis* is deeply tricolpate and reticulate (Martin & Drew), and essentially the same has been reported for *L. amoena* (Hewitt). The pollen tubes of *L. siphilitica* were found by Halsted (1886) to be variously expanded at the tips in material growing through the style, evidently in contrast to the usual condition in *Lobelia,* and the same was also later observed in *L. cardinalis* among pollen grains germinated in a sugar solution (Halsted, 1887). The tips of pollen tubes of *L. amoena* grown in a sugar solution were not expanded in illustrations provided by Hewitt, suggesting that tip expansion is not artificial and perhaps even indicative of a relationship between *L. cardinalis* and *L. siphilitica.*

Seed germination was studied in several species of *Lobelia* by Muenscher. Light was required by *L. inflata, L. siphilitica,* and *L. cardinalis,* but not by several extraregional species. However, although some of the seeds of *L. inflata* germinated after one year, all those obtained from *L. cardinalis* or *L. siphilitica* were dormant. Muenscher suggested that since the seeds of all species were air dried upon harvesting, an additional dormancy was induced in *L. cardinalis*

[14]The material studied by Hewitt was all obtained from localities outside the range of *L. amoena* var. *amoena* but within that given for var. *glandulifera* by McVaugh (1943).

and *L. siphilitica*; however, germination tests with fresh, undried seeds were not conducted. In view of the habitat differences between *L. inflata* (dry places) and these two species (wet places subject to periodic drying), a greater drought-induced seed dormancy in *L. cardinalis* and *L. siphilitica* could be seen as adaptive. Barton reported that seed longevity in *L. cardinalis* was increased by drier conditions, lower temperatures, and lower oxygen concentrations.

Baskin & Baskin conducted a detailed ecological investigation of *Lobelia Gattingeri,* an endemic of the limestone cedar glades in the Central Basin of Tennessee. Because its seeds can germinate in either autumn or spring, depending on environmental conditions at the time of seed maturation, the plant may behave as either a winter or a summer annual. Populations were found to be infrequent, as well as small, and to vary greatly in size from year to year, depending largely on seedling survival. Seedling mortality results from low temperatures in the winter and drought conditions in the summer.

Several species of *Lobelia* have horticultural and/or medicinal value; none is known to be a serious pest, although some are poisonous. Appalachian populations of *L. inflata* have provided the principal supply of lobeline, employed in therapy against tobacco use (about 300–400 pounds annually) and as a stimulant, antiasthmatic, and expectorant. Although attempts have been made to bring *L. inflata* into cultivation, it is evident that, compared to this species, *L. cardinalis* yields as much lobeline and *L. puberula* actually yields about 32 percent more (Krochmal *et al.,* 1970, 1972a). Lobeline has also been reported in other species of *Lobelia* (for references see Shah *et al.*).

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THE WEST INDIAN SPECIES OF PHORADENDRON (VISCACEAE)

E. A. KELLOGG AND R. A. HOWARD[1]

In this paper we attempt to delimit morphological units and typify names for the West Indian species of *Phoradendron.* Such a revision is critical for any future work in the genus because many of the oldest names have been given to Caribbean plants. The taxonomy of the genus has long been confused because of variability in taxonomic characters and widespread misapplication of names. This situation was aggravated by Trelease's (1916) monograph, which created more problems than it solved. Our study has been based primarily on examination of herbarium specimens at A, BM, GH, ILL, K, NY, and P (see APPENDIX for an index to specimens seen). Several of the species have also been observed during field work in the Lesser Antilles. In publishing this treatment, we trust that it will not be taken as the final word on Caribbean *Phoradendron.* Many problems have been uncovered that will only be resolved by additional field observation or experimental developmental studies. We hope, however, that by clearing away some of the nomenclatural debris and by noting which characters reliably distinguish taxa, we can provide a foundation for the work of future monographers.

We have included here all taxa native to the West Indian islands. We have also included all synonyms that have appeared in the literature on West Indian *Phoradendron,* although some of them refer to South American plants. This has forced us to venture opinions on some Central and South American species, even though we have not studied all these species in detail. This is an inevitable problem in a regional study; we have attempted to mitigate its effect by noting where our conclusions are tentative and need further examination.

In this treatment we have recognized as species discrete morphological units within which all characters vary and covary continuously. In some cases the range of continuous variation is quite broad. All taxa are recognized at the species level, purely as a matter of convention. To give two taxa varietal status implies a close relationship between them, and we feel that any statements of relationship are premature. For example, *Phoradendron gracile* (Krug & Urban) Trel. may be better treated as a variety of *P. quadrangulare* (Kunth) Griseb., but this depends in part on the relationships of the other South American species close to *P. quadrangulare.* We are therefore not publishing any new names or combinations, although some of the latter may ultimately be necessary if any species are reduced to varietal status. Except in the case of *P. carneum*

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Urban, for which we have seen only two specimens from Trinidad, our descriptions are based on Caribbean material; in this instance the description was augmented with measurements from Mexican material.

The West Indian species of *Phoradendron* were revised by Krug and Urban, and their treatment was published by Urban in 1897. They recognized 24 taxa in the region, of which nine are shared with South or Central America, 14 are endemic to the Caribbean islands, and one (*Phoradendron tetrastachyum* Griseb.) is actually a *Dendrophthora*. Nineteen years later, Trelease (1916) published his monumental work encompassing the entire genus *Phoradendron*. Trelease apparently had a much narrower concept of species than did Krug and Urban; he separated taxa of specific rank by unusually fine distinctions. In the West Indies he recognized 36 taxa, of which only three were shared with South America. Although both Trelease and Urban published a number of new species of *Phoradendron* after 1916, no one has since attempted to revise the West Indian species and to evaluate the substantial differences between Krug and Urban's and Trelease's treatments.

This treatment is in many respects similar to Krug and Urban's. We recognize 25 species, of which ten are endemic to the West Indies and the remainder are shared with Central and/or South America. The lower number of West Indian endemics partly reflects increased collecting and the great number of floristic studies that have been undertaken since the turn of the century. We have found four pairs of taxa (*Phoradendron undulatum* (Pohl) Eichler/*P. herminieri* Trel.; *P. quadrangulare* (Kunth) Griseb./*P. randiae* Bello; *P. crassifolium* (Pohl) Eichler/*P. martinicense* (DC.) Griseb.; *P. ottonis* Eichler/*P. caerulescens* Trel.) in which one (the first-listed) member is South American and one is Caribbean. For these pairs the South American name is older. If the two taxa in each pair are judged to be a single species, the South American name will take precedence and the Caribbean name will be relegated to synonymy. It is beyond the scope of this study, however, to analyze the full range of variation in the South American plants. We therefore point out these pairs of "species" as ones deserving further study. In our treatment of each, we have given the rationale for our taxonomic decision, but it should in all cases be regarded as preliminary.

GENERIC RELATIONSHIPS

Phoradendron is a genus of woody parasites distributed from New Jersey to Oregon and Utah in the United States and south to Argentina and Bolivia; its greatest diversity is in the tropics. Many of the species were originally described in *Viscum* L., from which *Phoradendron* was distinguished by Nuttall in 1848 on the basis of its three-merous (vs. four-merous) flowers and its spicate inflorescences (vs. flowers in axillary clusters). Engler (1894) placed *Phoradendron* in the tribe Phoradendreae, along with *Dendrophthora* Eichler. The only reliable character separating these two genera is the nature of the anthers—unilocular in *Dendrophthora* and bilocular in *Phoradendron*. This character is difficult to evaluate on herbarium specimens unless the flowers are boiled and dissected; we have found it to be consistent in all West Indian species of both genera. Other distinctions between the two genera are less reliable. Most plants with flowers arranged in a single vertical rank above the bract belong in *Dendro-*

phthora, but other inflorescence types appear in that genus as well (Kuijt, 1961). Kuijt (1961, p. 5) noted that "one develops an intuitive feeling of relationships after scrutinizing a large number of species, a feeling which allows one to be reasonably sure that a certain specimen belongs in *Dendrophthora* and not in *Phoradendron.*"

The Phoradendreae are members of the Viscaceae, a family distinguished from the Loranthaceae by numerous morphological, anatomical, and developmental characters (Kuijt, 1969, summarizing Barlow, 1964, and Dixit, 1962). Because some workers have suggested separate evolutionary origins for the Viscaceae and the Loranthaceae (Kuijt, 1968), we believe they should be recognized as separate families, rather than subfamilies.

CHARACTERS STUDIED

BRANCHING PATTERN. Plants vary in the frequency with which the shoot apex aborts or is terminated by inflorescences. Most West Indian species are monopodial, with the main axis continuing to grow and branching occurring only at the lower nodes. However, in three West Indian taxa (*Phoradendron dichotomum* (Bertero) Krug & Urban, *P. northropiae* Urban, and *P. racemosum* (Aublet) Krug & Urban) the apex almost invariably aborts, establishing a bifurcate branching pattern.

STEM SHAPE. Young stems in *Phoradendron* may be quadrangular and more or less winged (*P. tetrapterum* Krug & Urban), flattened and clearly two-edged (*P. anceps* (Sprengel) Krug & Urban), or nearly terete (*P. carneum* Urban). Many intergrading forms exist. For example, many flattened stems not only are two-edged in the plane of the leaves, but also have slightly less prominent ridges at right angles, giving the stem an approximately rhombic cross section. Furthermore, plants in most species become increasingly terete with age.

CATAPHYLLS. The West Indian members of the genus all bear reduced, bractlike cataphylls in addition to normal expanded foliage leaves. They are tightly appressed to the stem in fresh material but flare out on drying. The cataphylls may be fused to form what has been called a "vagina cataphyllaris," or they may be partially separate. Occasionally they have a prominent white margin. In West Indian members of *Phoradendron* (unlike the condition in some species of *Dendrophthora*), the first pair of cataphylls is generally in the plane opposite to that of the prophylls, giving the plants a strictly decussate phyllotaxy. Each lateral branch has, as its first appendages after the prophylls, one or more pairs of cataphylls. In some taxa (Trelease's sect. *Continuae*) additional pairs of cataphylls occur distal to each subsequent pair of foliage leaves, producing a pseudodistichous phyllotaxy. In the species descriptions, we record the distance of the cataphylls above "the node"; this refers to the node with a pair of expanded leaves immediately below the cataphylls.

The first pair of appendages on the inflorescence is a pair of prophylls; these are commonly minute but occasionally prominent. In the latter case we have noted it in the species descriptions. Cataphylls distal to the prophylls may or may not occur on the inflorescence; when they do, they are often similar in morphology to the bracts subtending the flowers.

LEAVES. Leaves may be nearly linear to suborbicular, symmetrical to notably gibbous or falcate, obtuse to acuminate, and wider from above to below the middle. They may dry green to black or sometimes reddish or almost fluorescent yellow (*Phoradendron flavens* (Sw.) Griseb.). Several of the taxa described in this paper (e.g., *P. wattii* Krug & Urban, *P. anceps*) are highly variable in leaf shape and size. Field observations in the Lesser Antilles have revealed substantial variation within a single plant; one specimen of *P. anceps* (*Howard et al. 18816*) bore leaves characteristic of four previously recognized "taxa." In addition, all intermediate shapes can be found connecting "taxa" previously delimited on leaf shape. A biosystematic study should address the lability of this character; we have found it to be much less reliable than past treatments of the genus would indicate.

Leaves may be basinerved or penninerved, although there are cases (particularly in herbarium specimens) where the distinction becomes difficult. The separation of the three main basal nerves may be somewhat above the base on some leaves. Trelease (1916) used this character to distinguish his sections *Basinervae* and *Penninervae*; while it is sometimes a useful character, it should not be weighted so heavily.

TYPE OF INFLORESCENCE. Through careful morphological and anatomical study, Kuijt (1959) has documented the variation in inflorescence pattern in some members of the Viscaceae, and his 1961 revision of *Dendrophthora* has shown how useful it can be taxonomically. In the Caribbean species of *Phoradendron,* we have found six types of inflorescence (FIGURE 1), including Kuijt's types 1a and 1b and modifications of them. The inflorescence in tribe Phoradendreae is an articulated structure with two opposite bracts subtending each fertile internode. Above each bract the flowers are most commonly arranged in two parallel columns, with a single apical flower placed midway between the columns (type 1a). In other plants there are three full columns of flowers above the bract (type 1b). In some plants the three columns are reduced to one flower each, producing a triad of flowers above each bract. As Kuijt has noted, the triad cannot be assigned to either type; however, its occurrence is consistent within certain taxa (e.g., *P. mucronatum* (DC.) Krug & Urban), so we will refer to it simply as a triad. We use these types merely as short-hand descriptions of inflorescence patterns; we do not claim that they are "real" in any developmental sense. Types 1d and 1e may simply represent slightly aberrant forms of 1a, but we name them for convenience in referring to them (e.g., in *P. anceps,* where they are common).

STAMINATE AND PISTILLATE FLOWERS. Plants may be monoecious or dioecious. If monoecious, staminate and pistillate flowers both occur on the same inflorescence. Within this inflorescence they may occupy separate internodes (e.g., in *Phoradendron solandrae* Proctor), in which case the staminate internodes are generally above the pistillate. If they occupy the same internode, their position in the internode may be variable or regular; if the latter (e.g., in *P. mucronatum*), generally the apical flower is staminate and the lower flowers pistillate.

FLOWER ORIENTATION. Eichler (1868) attempted to use orientation of the flowers

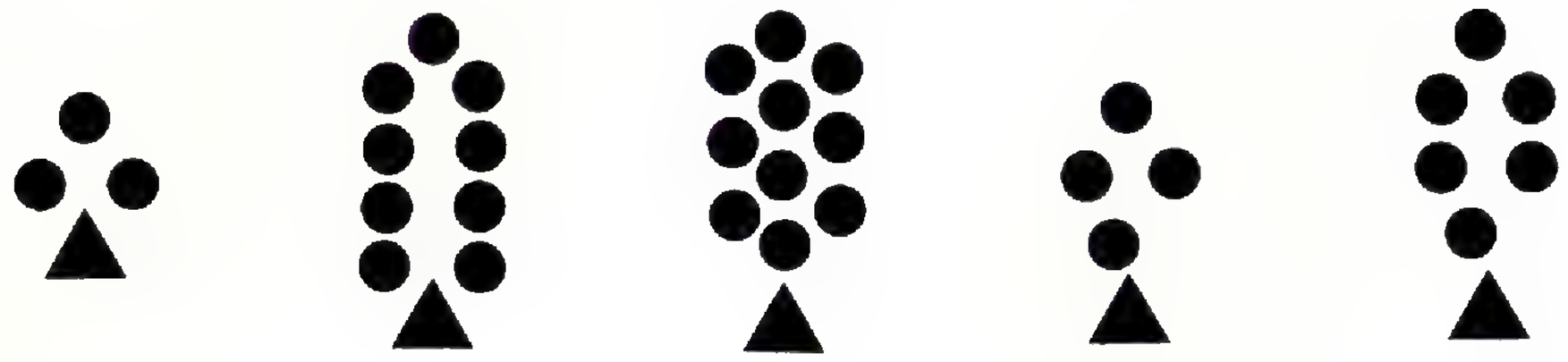

FIGURE 1. Inflorescence types (based on Kuijt, 1959). Type 1c inflorescence not found in West Indian species. Circles = flowers, triangles = bracts.

as a taxonomic character. One of the sepals is usually in line with the vertical axis of the inflorescence; if the central sepal is uppermost, then the flower is designated as "1/2," whereas if it is in the lower position the flower is designated as "2/1." Kuijt (1959) has shown that this character is not stable enough to be of much taxonomic value. It is, however, consistent within some inflorescence types. In 1a inflorescences, for example, the apical flower is generally 2/1, the lower ones 1/2.

SEPALS. The flowers of *Phoradendron* are extremely uniform, but whether the sepals are open or closed at fruit maturity is taxonomically useful information. If they are open (as in *P. trinervium* (Lam.) Griseb.), they stand erect and toothlike, making this character relatively easy to use on specimens with mature fruits.

FRUIT COLOR AND SHAPE. Fruit color varies from white through yellow to red and in some cases may be concordant with other characters. In general, however, mature fruits are absent from herbarium specimens, and collectors' notes frequently do not mention the character. Immature fruits may sometimes be helpful: in dry specimens of *Phoradendron anceps,* enlarging fruits have a distinct golden sheen when viewed under a 10× lens. Fruit shape has been mentioned in some descriptions but is difficult to use on herbarium specimens; *P. anceps* has notably pyriform young fruits, but other variations in fruit shape must be documented in the field. Some species (e.g., *P. mucronatum*) are characterized by warts on the pericarp. In other species (e.g., *P. gracile*) these warts do not appear on all fruits, and in still others (e.g., *P. trinervium*) the warts are reduced to an obscure ring around the fruit just below the sepals.

TAXONOMIC TREATMENT

Phoradendron Nutt. J. Acad. Nat. Sci. Philadelphia, ser. 2. **1:** 185. 1848.

Phoradendrum auct. sphalm.

Woody parasites with flattened, rhombic, quadrangular, or terete stems. West Indian species all with expanded foliage leaves, cataphylls on all axes or only on lateral branches. Leaves opposite, petiolate or sessile, basinerved or penninerved, frequently drying coriaceous. Plants monoecious or dioecious; if monoecious, then staminate and pistillate flowers on same inflorescence but

not necessarily in same fertile internode. Inflorescences spikes, with or without basal cataphylls; fertile internodes 2 to several, each subtended by pair of opposite, decussate bracts. Flowers in pits along rachis, arranged in 1 to 3 ranks above each bract, singly (then pistillate), in triads, or in more complex arrangements. Perianth parts (sepals) in single whorl of 3, these closed or open and erect in fruit. Staminate flowers shed soon after anthesis; anthers 3, sessile, bilocular. Pistillate flowers with short style and inferior ovary. Fruits ovoid to globose or pyriform, white, yellow, or red, smooth, papillate, wrinkled, or warty. Seed 1, surrounded by fibrous viscid endocarp.

TYPE SPECIES: *Phoradendron californicum* Nutt.

KEY TO THE WEST INDIAN SPECIES OF PHORADENDRON

1. At least 1 pair of cataphylls distal to each pair of foliage leaves (on both main axes and laterals).
   2. Axes not terminated by an inflorescence; branching not bifurcate (plant monopodial).
      3. Leaves with 3 to 5 (to 7) basal or nearly basal nerves; inflorescences type 1b or triads.
         4. Inflorescences triads, formed in axils of cataphylls. . . 13. *P. martinicense.*
         4. Inflorescences type 1b, not in axils of cataphylls. . . . . 5. *P. flavens.*
      3. Leaves penninerved; inflorescences type 1a. . . . . 17. *P. piperoides.*
   2. Axes terminated by an inflorescence, branching thus appearing bifurcate.
      5. Leaves basinerved, nerves generally prominent.
         6. Sepals open, erect on mature fruits. . . . . 12. *P. inequidentatum.*
         6. Sepals closed on mature fruits. . . . . 4. *P. dichotomum.*
      5. Leaves penninerved, nerves obscure.
         7. Largest leaves < 6 cm long; fruits red; Bahamas. . . . 15. *P. northropiae.*
         7. Largest leaves > 8 cm long; fruits white; Hispaniola and Puerto Rico. . . . . 19. *P. racemosum.*
1. Cataphylls only at base of lateral branches.
   8. Stems 4-winged; inflorescences type 1a; fruits white. . . . . 22. *P. tetrapterum.*
   8. Stems terete, compressed, or 4-ridged, but not winged; inflorescence type and fruits various.
      9. Leaves strap shaped, their bases meeting; fruits warty throughout, set in spreading cup with glandular margin. . . . . 3. *P. carneum.*
      9. Leaves not as above, petiole more or less well-developed; fruits warty or not; spreading cup, if present, lacking glandular margin.
         10. Flowers 1 per bract (2 per fertile internode).
            11. Leaves wider above middle, obovate to oblanceolate, basinerved; fruits drying dark or light, but not glaucous with paler sepals. . . . . 23. *P. trinervium.*
            11. Leaves wider at or below middle, lanceolate to elliptic or oblong (only rarely oblanceolate), penninerved; fruits drying dark, glaucous, with paler sepals. . . . . 25. *P. wattii.*
         10. Flowers more than 1 per bract.
            12. Inflorescence internodes appearing tetrastichous with 4 pistillate flowers (flowers actually in 2 triads, each triad with upper flower staminate, lower 2 pistillate); fruits warty throughout.
               13. Leaves suborbicular, glaucous; Trinidad. . . . . 16. *P. ottonis.*
               13. Leaves obovate to oblanceolate, not glaucous; widespread. . . . . 14. *P. mucronatum.*

12. Inflorescence internodes with more than 4 pistillate flowers (if flowers in triads, then pistillate flower uppermost or entire internode unisexual); fruits smooth or wrinkled, or warty only on upper part.
    14. Inflorescences type 1b, prominently hexastichous, clavate.
        15. Most flowers pistillate, forming white fruits; bracts forming bilobed "cup"; leaf margin slightly revolute. . . . . 11. *P. hexastichum.*
        15. All flowers staminate (pistillate plants of this species have inflorescence type 1a); bracts fully fused to form cup with horizontal rim; leaf margin plane. . . 7. *P. grisebachianum.*
    14. Inflorescences type 1a, 1d, 1e, or triads, slender, linear.
        16. All flowers in triads.
            17. Leaves penninerved; sepals closed in mature fruit.
                18. Leaf apex acute to acuminate, apiculate; only pistillate flowers borne in upper half of fertile internode. . . . . 7. *P. grisebachianum.*
                18. Leaf apex rounded to obtuse, not apiculate; both staminate and pistillate flowers borne throughout fertile internode. . . . . 8. *P. gundlachii.*
            17. Leaves basinerved; sepals open and erect in mature fruit.
                19. Stem flattened, flaring below nodes; internodes often < 3 cm long; fruits red-orange to scarlet; Cuba and Bahamas. . . . . 20. *P. rubrum.*
                19. Stem quadrangular, not flaring; internodes often > 3 cm long; fruits yellow to orange or red-orange; Antilles other than Cuba. . . . . 23. *P. trinervium.*
        16. Inflorescences type 1a, 1d, or 1e, at most only few inflorescences on plant triads.
            20. Leaves > 3 times as long as wide, lance-linear to oblanceolate.
                21. Some fruits warty above; leaves < 1 cm wide. . . . . 6. *P. gracile.*
                21. Fruits smooth; leaves various.
                    22. Leaf apex rounded. . . . . 9. *P. haitense.*
                    22. Leaf apex apiculate.
                        23. Young fruits drying with golden sheen, pyriform. . . . . 10. *P. hartii.*
                        23. Young fruits drying dark, only obscurely (if at all) golden, globose to oblong. . . . . 18. *P. quadrangulare.*
            20. Leaves < 3 times as long as wide, shape variable.
                24. Dry immature fruits pyriform or lageniform, with golden sheen when viewed under 10× lens. . . . . 1. *P. anceps.*
                24. Dry immature fruit globose or cylindrical, not golden.
                    25. Largest leaves ≥ 8 cm long.
                        26. Leaf apex acuminate. . . . . 24. *P. undulatum.*
                    26. Leaf apex rounded, sometimes apiculate.
                        27. Fertile internodes narrowly cylindrical, not flaring distally; flowers 7 to 15 per bract; Cuba, Hispaniola, and Puerto Rico. . . . . 2. *P. barahonae.*

27. Fertile internodes strongly clavate, distally flaring; flowers 3 to 5 per bract; Jamaica. . . . . 21. *P. solandrae.*

25. Largest leaves < 6.5 cm long.

28. Leaves basinerved; sepals open, erect in mature fruit; fruits yellow, orange, or red. . . . . See couplet 18.

28. Leaves penninerved; sepals closed in mature fruit, or opening only slightly; fruits white. . . . . See couplet 17.

1. **Phoradendron anceps** (Sprengel) Krug & Urban *in* Urban, Bot. Jahrb. Syst. **24:** 41. 1897. FIGURE 2a, b.

Viscum anceps Sprengel, Syst. Veg. ed. 16 [17]. **1:** 487. [1824] 1825. TYPE: Santo Domingo, *Bertero 439, pro parte* (lectotype (Trelease, 1916), B, destroyed; isolectotypes, G-DC, IDC 800. 664: I. 3 (left)!, PR; photo of PR specimen at ILL!).

Viscum flavens Sprengel, *ibid.* 488, *pro parte*; not Sw. 1788. ?*Phoradendron flavens* Eggers, Fl. St. Croix, 123. 1876; Fl. St. Croix & Virgin Is. 59. 1879; not Griseb. 1860. TYPE: Porto Rico, 1820, *Bertero s.n.* (holotype, B, destroyed; isotype, G-DC, IDC 800. 664: I. 7!).

Phoradendron martinicense sensu Griseb. Fl. Brit. W. Indian Is. 314. 1860, *pro parte* (as to *Imray 217* from Dominica, *fide* Nicolson (unpubl. MS)).

Phoradendron chrysocarpum Krug & Urban *in* Urban, Bot. Jahrb. Syst. **24:** 39. 1897.

Phoradendron chrysocarpum Krug & Urban var. *typicum* Trel. *in* Stehlé, Bull. Soc. Bot. France **1953-54:** 27. 1954. TYPE: Porto Rico, *Bertero 439, pro parte* (lectotype (Trelease, 1916), G-DC, IDC 800. 664: I. 3 (right)!).

Phoradendron crenulatum Urban, Symb. Antill. **5:** 332. 1907. TYPE: Jamaica prope Halberstadt, *Harris 6659* (holotype, B, destroyed, photo at ILL!; isotypes, BM!, NY!).

Phoradendron chrysocarpum Krug & Urban var. *dussii* Urban, *ibid.* 333. *Phoradendron dussii* (Urban) Trel. Genus *Phoradendron,* 100. 1916. *Phoradendron dussii* (Urban) Trel. var. *typicum* Stehlé, Bull. Soc. Bot. France **92:** 262. 1945. TYPE: Guadeloupe, *Duss 3904, pro parte* (holotype, B, destroyed, photo at ILL!; isotype, NY!; specimen at US is holotype of *P. herminieri* Trel.).

Phoradendron albovaginatum Urban, Symb. Antill. **7:** 504. 1913. TYPE: Jamaica prope Ewarton, *Harris 6703* (holotype, B, destroyed; isotype, NY!).

Phoradendron helleri Trel. Genus *Phoradendron,* 100. 1916. TYPE: Puerto Rico, E of Ponce, 3 Dec. 1902, *Heller 6188* (holotype, NY!, photo at ILL!; isotypes, GH!, US; photo of US specimen at ILL!).

Phoradendron cauliflorum Trel. Repert. Spec. Nov. Regni Veg. **26:** 343. 1929, from description. TYPE: Haiti, Morne Rochelois prope Miragone ad Icard cr., 750 m alt., *Ekman H6492* (holotype, B, destroyed).

Phoradendron dussii (Urban) Trel. var. *pauli* Stehlé, Bull. Soc. Bot. France **92:** 262. 1945. TYPE: Guadeloupe, *Bena, Quentin, & Stehlé 5834* (holotype, P?, not found; isotype, NY!).

Phoradendron chrysocarpum Krug & Urban var. *parvifolium* Trel. *in* Stehlé, *ibid.* TYPE: Martinique, Tunnel des Deux-Choux, 23 March 1939, *H. & M. Stehlé 3368* (holotype, ILL!; isotype, NY!).

Phoradendron berterianum sensu Bello, Apuntes Fl. Puerto-Rico **1:** 278. 1881, *fide* Urban (1897); not Griseb. 1860, or Eichler, 1868.

Stems flattened, ancipital, sometimes more or less rhombic; cataphylls 1 or 2 pairs, ca. 2 mm above node, at base of lateral branches only, scarcely fused, flaring ovate or truncate, white edged. Leaves with petiole 5–10 mm long; blade

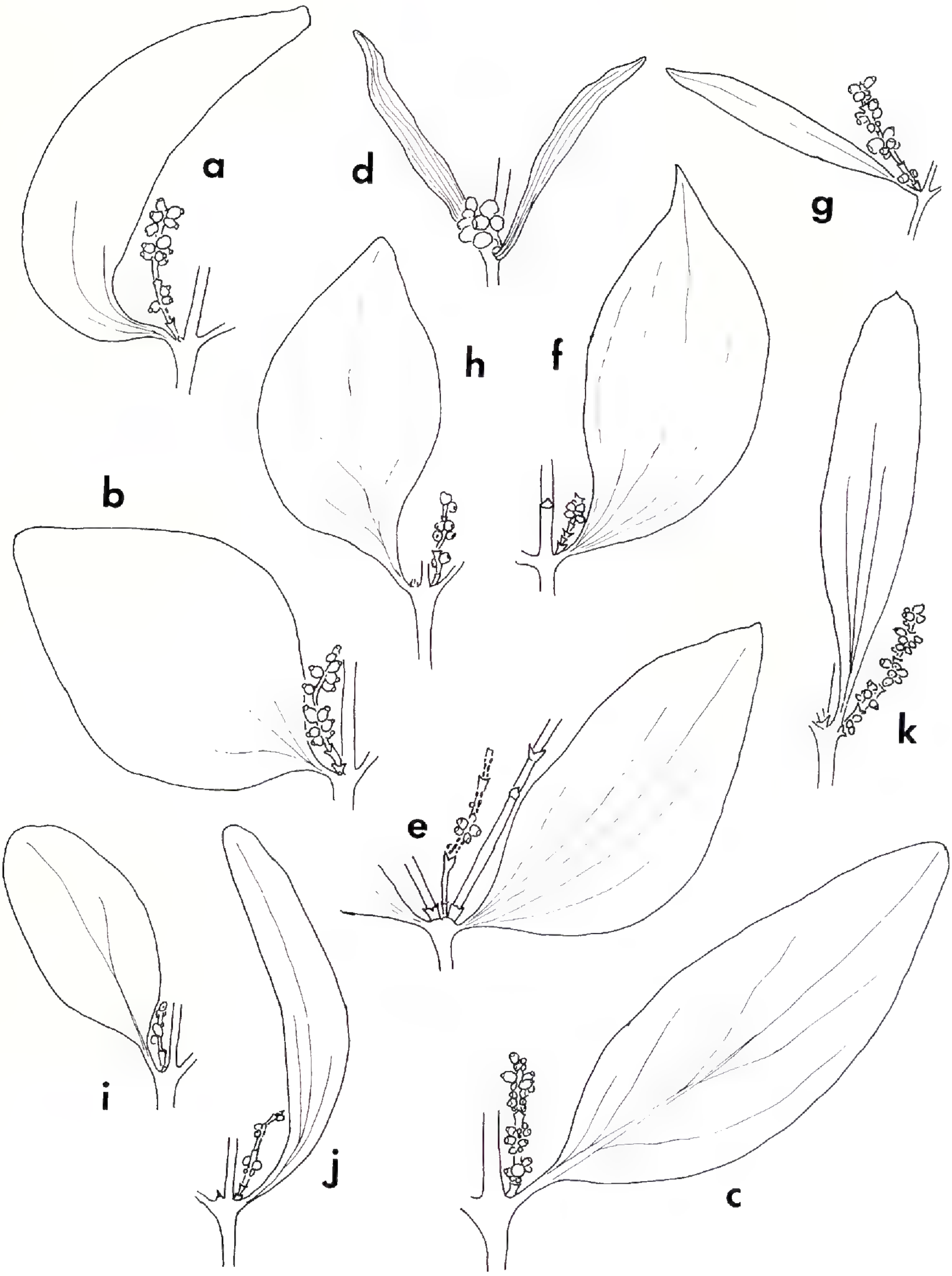

FIGURE 2. Leaves and inflorescences, × 0.53. a, b, *Phoradendron anceps*: a, *Ekman 9615* (GH); b, *Duss 101* (GH). c, *P. barahonae, Fuertes 927* (A). d, *P. carneum, Eggers s.n.*, 12/83 (GH). e, *P. dichotomum, Sintenis s.n.*, 12/85 (GH). f, *P. flavens, Wilbur 7973* (GH). g, *P. gracile, Rehder s.n.*, 15 Feb. 1903 (A). h, *P. grisebachianum, Harris 10861* (GH). i, *P. gundlachii, Wright 2650* (GH). j, *P. haitense, Ekman 9604* (GH). k, *P. hartii, Wiles W30* (K).

ovate, elliptic, or lanceolate, sometimes laterally asymmetric or falcate, 2.7–11.5(–13.5) × (1.1–)1.7–5.9 cm, apex obtuse, base cuneate, nerves all basal or laterals slightly suprabasal. Inflorescences 2 to 5 per leaf axil, to 4 cm long, axis ca. 1 mm thick when dry; cataphylls lacking or 1 pair, these and lower bracts 3-lobed; upper bracts more nearly entire and navicular, prominently white margined; fertile internodes 1 to 4, type 1d or 1e, less frequently type 1a or triads (or on upper internodes single pistillate flower per bract); flowers 3 to 12 per bract, unisexual or with staminate and pistillate flowers intermixed; apical flower 2/1, lower ones 1/2. Young fruits pyriform, drying with golden sheen visible under 10× lens; mature fruits creamy white to yellowish; sepals partially open but not stiffly upright at maturity.

DISTRIBUTION. Venezuela, Cuba, Hispaniola, Jamaica, Puerto Rico, St. Thomas, St. Croix, Guadeloupe, Dominica, Martinique, St. Lucia, St. Vincent, Trinidad.

Phoradendron anceps has been divided into several species distinguished on the basis of leaf shape. Our field observations, however, have shown that leaf shape is so variable even within a single individual that the distinctions among the taxa break down. Also, all inflorescence types can be found on a single plant. *Phoradendron dussii* var. *pauli,* from the Lesser Antilles, and *P. albovaginatum,* from Jamaica, appear to be small-leaved forms of *P. anceps. Phoradendron anceps* is similar to *P. haitense* and *P. hartii,* which are distinguished by their much longer, narrower leaves.

Phoradendron helleri var. *sanguinea* Trel. is better referred to *P. barahonae.*

2. **Phoradendron barahonae** Urban & Trel. Repert. Spec. Nov. Regni Veg. **13:** 444. 1914. TYPE: Hispaniola, *Fuertes 275, pro parte* (B, destroyed; lectotype (here designated), G, photo at ILL!; isolectotypes, A!, NY!, P!) (excluding *Fuertes 275* at BM!, GH!, K!, which is *Phoradendron racemosum*). FIGURE 2c.

Phoradendron cerinocarpum C. Wright ex Trel. Genus *Phoradendron,* 139. 1916, *nomen illegit.*

Phoradendron helleri Trel. var. *sanguinea* Trel. *ibid.* 100. TYPE: Hispaniola, *Fuertes 1531b* (holotype, B, destroyed, photo at ILL!; isotypes, GH!, NY!).

Stems flattened when young but rapidly becoming terete; cataphylls 1 or 2 pairs, on lateral branches only, 1–2 and 5 mm above node, subannular, white margined. Leaves with petiole 5–10 mm long; blade lanceolate, somewhat falcate, 4.4–15 × 1.4–5.5 cm, the apex tapering but ultimately obtuse, the base cuneate, the lateral nerves with 1 pair basal and 1 pair suprabasal, or all basal (Puerto Rico). Inflorescences 1 to 4 per leaf axil, more or less clavate, to 4 cm long, ca. 2 mm thick when dry; cataphylls lacking or 1 pair, like bracts entire or 3-lobed, flaring, forming infundibular tube; fertile internodes 3 to 5, type 1a; flowers 7 to 15 per bract, deeply sunken into rachis, unisexual or with staminate and pistillate flowers intermixed; apical flower 2/1, lower ones mostly 1/2, occasionally 2/1. Fruits globose, white; sepals closed.

DISTRIBUTION. Venezuela, Cuba, Hispaniola, Puerto Rico, St. Lucia.

Although it is somewhat inconvenient to lectotypify a species with a representative of a mixed collection, *Fuertes 275* at G is the only extant specimen that was definitely seen by the authors of the species.

The Puerto Rican plants are more consistently basinerved than are plants from elsewhere in the range. The one collection from St. Lucia (*Proctor 18089*) is unusual in that many of the fertile internodes have type 1b rather than type 1a inflorescences; however, fruit shape and texture and leaf shape and nervation all suggest placement in this species.

Phoradendron barahonae is similar to *P. anceps* but is often more clearly penninerved and tends to have more robust inflorescences with more flowers per internode. The fruits of *P. barahonae* are globose and somewhat flattened apically; the sepals often dry a color different from the rest of the fruit. In *P. anceps* the fruits are always pyriform until maturity, when they become globose but not flattened; the sepals are generally the same color as the fruit. The fruits of *P. anceps* have a pronounced golden sheen (visible under a 10× lens) when young, whereas those of *P. barahonae* are never golden. Trelease (1916), in his description of *P. cerinocarpum,* and Léon and Alain (1951) recorded the fruit color as red, but data on all specimens we have seen list it as white.

3. **Phoradendron carneum** Urban, Bot. Jahrb. Syst. **23:** 1. 1897. TYPE: Mexico, Jalisco, hills near Guadalajara, 1888, *Pringle 1854* (holotype, B, destroyed; isotypes, GH!, NY!). FIGURE 2d.

Stems flattened, rough-striate; internodes flaring above; prophylls prominent; cataphylls 1 pair on lateral branches only, basal, scarcely fused, thick, fleshy, acute. Leaves sessile; blade linear, straplike, 4.8–7.5 × 0.5–0.7 cm, apex obtuse, bases meeting, nerves all basal. Plants dioecious; inflorescences 1 or 2 per leaf axil, to 2.5 cm long, axis ca. 2 mm thick when dry; cataphylls lacking; prophylls prominent; bracts nearly fused, forming infundibular tube; fertile internodes 2, type 1a; flowers 5 to 11 per bract, orientation irregular. Fruits globose, in spreading cup with papillate margins, red-orange, warty, sepals closed.

DISTRIBUTION. Mexico (Guanajuato, Jalisco, Michoacán, Oaxaca, Puebla, Querétaro), Trinidad.

There are two possible explanations for the apparent disjunction: if the species has often been misidentified in herbaria the range may be more continuous than is evident here; or the two Trinidad specimens may be mislabeled. Both collected by Eggers, they are dated 12/83 and 2/83 but are otherwise unnumbered. Most of Eggers's other Caribbean collections are numbered. Eggers was in Trinidad in 1883, but he had been in Veracruz and Oaxaca from April 1865 to November 1867 when he was in the Danish army. Urban (1902) did not discuss any Eggers collections from Mexico, but these "Trinidad" specimens may have actually been collected while Eggers was in Oaxaca or traveling through southern Mexico after his discharge from the army.

4. **Phoradendron dichotomum** (Bertero) Krug & Urban *in* Urban, Bot. Jahrb. Syst. **24:** 48. 1897. FIGURE 2e.

Viscum dichotomum Bertero *in* Sprengel, Syst. Veg. ed. 16 [17]. **1:** 488. [1824] 1825, excluding synonyms and distribution in North America; not D. Don, 1825 (= *Viscum articulatum* Burman var. *dichotomum* Kruz ex Hooker, 1886) or *Loranthus dichotomus* Ruiz & Pavon, 1802 (= *Psitticanthus*). LECTOTYPE (Trelease, 1916): Santo Domingo, *Bertero 710* (PR, photo at ILL!).

Viscum berterianum DC. Prodr. Syst. Nat. Regni Veg. **4:** 281. 1830. *Phoradendron berterianum* (DC.) Griseb. Fl. Brit. W. Indian Is. 313. 1860 (as to name only—*P. berterianum* Griseb. = *P. grisebachianum* Eichler). TYPE: Santo Domingo, 1821, *Bertero s.n.* (G-DC, IDC 800. 663: III. 3!).

Phoradendron martinicense sensu Griseb. *ibid.* 314, *pro parte* (as to *Wright 1251*).

Phoradendron dichotomum (Bertero) Krug & Urban var. *ovatifolium* Krug & Urban *in* Urban, Bot. Jahrb. Syst. **24:** 49. 1897. *Phoradendron ovatifolium* (Krug & Urban) Urban, Symb. Antill. **8:** 188. 1920. TYPE: "in Sto. Domingo in sylvis Sierra del Palo Quemado 600 m. alt.," *Eggers 1845* (holotype, B, destroyed, photo at ILL!; isotypes, BM!, K!).

Phoradendron anceps sensu G. Maza, Anal. Inst. Seg. Enseñ. Habana **2:** 170. 1895, *fide* Urban (1897); not (Sprengel) Krug & Urban, 1897.

Stems flattened to terete, drying with characteristic long wrinkled furrows; branching bifurcate; cataphylls 1 or 2 pairs between pairs of foliage leaves, lower pair just above node, upper pair 1–3 cm above first, separate or slightly fused, broadly ovate to deltate, often white margined. Leaves with petiole indistinct, < 5 mm long; blade ovate, elliptic, or lanceolate, 4.6–12.5 × 2.4–6 cm, thin, apex acute to acuminate, base cuneate, nerves basal and prominent. Inflorescences terminal or axillary, in fascicles of 1 to several, up to 7 cm long, axis 2–4 mm thick when dry; cataphylls 1 or 2 pairs, cupuliform like bracts; basal internode sterile, to 8 mm long; fertile internodes 4 to 7, varying from type 1a to type 1b, both types on same plant, or upper part of internode type 1a and lower part hexastichous; flowers 14 to 21 per bract; internodes with staminate flowers above, pistillate below; apical flower 2/1, lower ones 1/2 or irregular. Fruits globose, white; sepals closed.

DISTRIBUTION. Panama, Cuba, Hispaniola, Jamaica, Puerto Rico.

The Jamaican members of this species have rounder leaves and only six to ten flowers per internode. One collection from San Juan Province, Dominican Republic (*Howard & Howard 8732*) has leaves with an obtuse apex, but in other respects it matches the species description.

Viscum dichotomum Bertero ex Sprengel was actually published in late 1824, according to Van Steenis-Kruseman and Stearn (1954) and so takes precedence over *V. dichotomum* D. Don, which was published on 1 February 1825 (Stearn, 1945).

5. **Phoradendron flavens** (Sw.) Griseb. Fl. Brit. W. Indian Is. 313. 1860. FIGURE 2f.

Viscum flavens Sw. Nova Gen. Sp. Pl. Prodr. 32. 1788, excluding *Viscum aliud racemosum, foliis latissimis* Plumier (= *Phoradendron hexastichum*) and *V. racemo-*

sum Aublet (= *P. racemosum*); not Sprengel, [1824] 1825, or Macfad. 1850. TYPE: Jamaica, *Swartz s.n.* (holotype, S, not seen; isotype, BM!).

Viscum macrophyllum Macfad. Fl. Jamaica **2:** 195. 1850; not Sprengel, [1824] 1825, or DC. 1830 (both = *P. racemosum*), or *Phoradendron macrophyllum* Ule, 1915. TYPE: Jamaica, *Macfadyen s.n.* (K!).

Phoradendron flavum Eichler *in* C. Martius, Fl. Brasil. **5**(2): 106. 1868. Error for *P. flavens* (Sw.) Griseb.

Phoradendron flavens (Sw.) Griseb. var. *australe* Trel. Genus *Phoradendron,* 155. 1916. TYPE: St. Vincent, *Eggers 6746* (location of holotype not designated, not at ILL; isotype, P!).

Phoradendron chrysocladon A. Gray, U. S. Expl. Exped., Phan. **15:** 743. 1854. TYPE: Brazil, near Rio de Janeiro, 1838–1842, *Wilkes Exped. s.n.* (holotype, US; isotype, GH!).

Stems flaring and somewhat flattened above, sometimes ribbed below leaves; cataphylls 1 or 2 pairs between each pair of foliage leaves, 1–2 cm above node (to 4 cm at base of lateral branches), not fused, large and flaring, deltate. Plants drying fluorescent yellow. Leaves with petiole indistinct; blade ovate to elliptic, often oblique, 5.2–16 × 2.2–8.5 cm, the apex acute to acuminate, the base cuneate, the nerves basal, prominent, reticulate adaxially. Inflorescences 1 to 3 per leaf axil, to 6 cm long, axis ca. 2 mm thick when dry; cataphylls 2 or 3 pairs, large, flaring like bracts; fertile internodes 3 to 5 (to 7), type 1b, flowers 11 to 18 per bract, staminate and pistillate intermixed; all flowers 1/2. Fruits globose, white to yellowish, drying rough-wrinkled; sepals closed.

DISTRIBUTION. Central and South America, Jamaica, Hispaniola, Guadeloupe, Dominica, St. Lucia, St. Vincent, Grenada, Trinidad.

Phoradendron flavens var. *australe* is the name applied by some authors to small-leaved plants of *P. flavens*; on the type specimen at P, the largest leaves are 6.5 × 2.5 cm. However, we have found that variation in leaf size is continuous within the species; *P. flavens* var. *australe* is not a discrete taxon.

Nicolson (unpublished MS) claims that the inflorescences have up to 12 joints. We have seen no specimens with this many fertile internodes.

6. **Phoradendron gracile** (Krug & Urban) Trel. Genus *Phoradendron,* 112. 1916. FIGURE 2g.

Phoradendron quadrangulare (Kunth) Krug & Urban var. *gracile* Krug & Urban *in* Urban, Bot. Jahrb. Syst. **24:** 37. 1897. *Phoradendron rubrum* Griseb. var. *gracile* (Krug & Urban) Fawcett & Rendle, Fl. Jamaica **3:** 96. 1914. TYPE: Jamaica, 1896, *Harris 6392* (lectotype (Trelease, 1916), B, destroyed, photo at ILL!; isolectotype, NY!).

Phoradendron gracile (Krug & Urban) Trel. var. *ballii* Trel. Genus *Phoradendron,* 113. 1916. TYPE: Jamaica, 1882, *Ball s.n.* (holotype, B, destroyed, photo at ILL!).

Stems rhomboid to quadrangular; cataphylls 1 pair at base of lateral branches only. Leaves with petiole < 5 mm long; blade oblong-linear, 3.3–6.5 × 0.5–0.9 cm, the apex obtuse to acute, sometimes apiculate, the base tapering, the nerves basal. Inflorescences 1 or 2 per leaf axil, to 4 cm long, axes 1 mm thick when dry; cataphylls lacking; fertile internodes 3 to 5, type 1a; flowers 7 to 9

per bract; internodes staminate, pistillate, or mixed; apical flower 2/1, lower ones 1/2. Fruits globose, color not reported, at least some rough-wrinkled or warty-tuberculate before maturity; sepals closed.

DISTRIBUTION. Cuba, Jamaica.

Krug and Urban (*in* Urban, 1897) reported plants with 11 to 15 flowers per bract.

This taxon should perhaps be returned to varietal status under *Phoradendron quadrangulare.* Development of warty fruits is a consistent character for distinguishing other taxa in the genus, however, so we have weighted it more heavily than some authors have. Developmental and genetic studies would be helpful here to determine the likelihood of parallel evolution of warty fruits.

7. **Phoradendron grisebachianum** Eichler *in* C. Martius, Fl. Brasil. **5**(2): 127, 134m. 1868. FIGURE 2h.

Phoradendron berterianum (DC.) Griseb. Fl. Brit. W. Indian Is. 313. 1860, excluding plant from St. Vincent, which is *P. hexastichum.* In his description of *P. berterianum,* Grisebach cited *Alexander s.n., McNab s.n., Purdie s.n., and Macfadyen s.n.,* all from Jamaica. Krug and Urban (*in* Urban, 1897) claimed that these were not in Grisebach's herbarium at Göttingen but at K, where Grisebach is known to have worked. Of the four, we found only the Alexander specimen, which we designate as the lectotype. Trelease neotypified the species with *Harris 6341* (GH!, NY!), but this neotypification is superseded by the discovery of authentic material at K.

Phoradendron fici Urban, Symb. Antill. **5:** 333. 1907. TYPE: Jamaica, Great Goat Island, alt. 50′, 19 April 1906, *Harris 9220* (holotype, B, destroyed, photo at ILL!; isotypes, BM!, NY!).

Stems flattened to rhombic, somewhat flaring above; cataphylls 1 or 2 pairs, at base of lateral branches only, lower pair 1–2 mm above node, second pair 5–10 mm above first, flaring-ovate and scarcely fused to subannular. Leaves with petiole 6–12 mm long; blade lanceolate to lance-elliptic, 5–14 × 1.5–4.5 (–7.5) cm, membranaceous, apex acute to sharply acuminate and apiculate, base cuneate, nerves pinnate. Plants dioecious; inflorescences 1 to 5 per leaf axil, to 3.5 mm long, axis < 1 mm thick when dry; cataphylls lacking or 1 pair, fused with bracts to form straight horizontal collar; fertile internodes 3 or 4, on pistillate plants type 1d or triads, with flowers 3 to 5 per bract, apical flower 2/1, lower ones 1/2, on staminate plants type 1b, with flowers 10 to 13 per bract. Fruits borne in top half of fertile internode, globose, red to red-orange, drying distinctively rough-wrinkled; sepals closed.

DISTRIBUTION. Endemic to Jamaica.

Léon and Alain (1951) reported that this species was cited by Urban (no reference given) as having been collected by Paul Serre in 1909 in the province of Habana. We have seen no Cuban specimens and believe that the report may be in error.

Some specimens of this species may be confused with those of *Phoradendron hexastichum.* The leaves are very similar in size, shape, and venation, but those of *P. grisebachianum* are more membranous and are generally smaller. The

pistillate spikes of the two species are not at all alike. In *P. grisebachianum* they are slender with three or four fertile internodes; the flowers are mostly in triads borne well above the midpoint of the internode and produce red to red-orange berries that dry rough-wrinkled. In *P. hexastichum* they are thick and clavate with four or five fertile internodes; the flowers are in a type 1b arrangement and extend to the bottom of the internode, producing white berries that dry more or less smooth and blackish. The confusion is created by the staminate spikes, which are type 1b in both species. The only difference between the two that we have been able to discover is that the members of a pair of bracts in *P. grisebachianum* are fused to form a straight-edged flaring cup and are not at all distinguishable; in *P. hexastichum* the "cup" is clearly bilobed and frequently white margined. Also, because *P. hexastichum* is monoecious, developing fruits are present on all but very young specimens. Defined in this way, the two species have nonoverlapping ranges: *P. grisebachianum* is endemic to Jamaica, whereas *P. hexastichum* does not appear to occur on that island.

8. **Phoradendron gundlachii** Krug & Urban *in* Urban, Bot. Jahrb. Syst. **24:** 44. 1897. TYPE: "habitat in Cuba in summitate Guayabon m. Jun.," *C. Wright 2650* (holotype, B, destroyed; isotypes, G, GH!, K!; photo of G specimen at ILL!). FIGURE 2i.

"*Phoradendron flavescens forma foliis majoribus,*" Griseb. Catal. Pl. Cubens. 120. 1866; not *P. flavescens* Nutt. Type the same as for *P. gundlachii.*

Stems flattened, rapidly becoming terete; cataphylls 1 or 2 pairs at base of lateral branches only, second pair < 1 cm above first, ovate, spreading. Leaves with petiole 4–9 mm long; blade elliptic to ovate, 4.6–6.5 × 1.6–4.5 cm, apex rounded to obtuse, base cuneate, nerves obscure, 3 basal veins and 2 lateral veins joining midvein above base. Inflorescences solitary in leaf axils, to 3 cm long, axis ca. 1 mm thick when dry; cataphylls 1 pair; bracts shallowly cleft and white margined; fertile internodes 2 or 3, type 1d, 1e, or triads; flowers 3, 4, or 6 per bract; pistillate only or both sexes intermixed; flower orientation irregular. Fruits globose, white; sepals closed.

DISTRIBUTION. Endemic to Cuba.

See discussion under *Phoradendron rubrum.* Urban (1897) noted that this species is very similar to *P. acinacifolium* C. Martius.

9. **Phoradendron haitense** Urban, Symb. Antill. **5:** 334. 1907. LECTOTYPE (Trelease, 1916): Haiti, ad Petite Rivière de l'Artibonite, *Picarda 1666* (B, destroyed, photo! in Trelease, 1916, *pl. 135*). FIGURE 2j.

Stems flattened; cataphylls 1 pair at base of lateral branches only, not fused, ovate. Leaves with petiole 5 mm long; blade lance-linear to oblanceolate, often somewhat falcate, 5–12 × 1–2 cm, the apex acute to truncate, often mucronate, the base tapering, the nerves basal. Inflorescences 1 per leaf axil, to 3 cm long, axis ca. 1 mm thick when dry; cataphylls lacking or 1 pair, like bracts flaring, navicular, entire, and white margined; fertile internodes generally 2, type 1d

or 1e (1a); flowers 4 to 7 per bract; apical flower 2/1, lower ones 1/2. Young fruits pyriform, with golden sheen visible under 10× lens when dry; color of mature fruits not recorded; sepals partially open.

DISTRIBUTION. Endemic to Hispaniola.

This species is distinguished from *Phoradendron anceps* by its narrower leaves, and from *P. hartii* by its flattened stems and rounded leaf apices.

10. **Phoradendron hartii** Krug & Urban *in* Urban, Bot. Jahrb. Syst. **24:** 40. 1897. TYPE: Trinidad ad St. Anne's, 8/1896, *Hart 6101* (holotype, B, destroyed, photo at ILL!; isotype, P!). FIGURE 2k.

Stems terete to compressed; cataphylls 1 pair on lateral branches only, ca. 1 mm above node, separate, flaring, broadly ovate. Leaves with petiole 5–10 mm long, distal end indistinct; blade lance-linear to oblong, somewhat falcate, 6–13.6 × 1.3–3.2 cm, apex rounded to more often acute with apical thickening 1 mm long, base tapering, nerves all basal or inner ones suprabasal. Inflorescences 1 to 4 per leaf axil, 2–3 cm long, axis ca. 1 mm thick when dry; cataphylls 1 pair, they and bracts 3-lobed to entire, white margined, navicular; fertile internodes 3 to 6, type 1a or 1e; flowers 3 to 7 per bract, mostly pistillate but some internodes with staminate and pistillate intermixed; apical flower 2/1, lower ones 1/2. Young fruits pyriform, drying with golden sheen visible under 10× lens; color of mature fruits not reported; sepals closed.

DISTRIBUTION. Dominica, Trinidad.

This species is distinct from *Phoradendron quadrangulare* on the basis of its fruit (golden, pyriform), and from *P. anceps* because of its long, slender (more than three times as long as wide) leaves and acute apical thickenings.

11. **Phoradendron hexastichum** (DC.) Griseb. Fl. Brit. W. Indian Is. 313. 1860. FIGURE 3a.

Viscum hexastichum DC. Prodr. Syst. Nat. Regni Veg. **4:** 282. 1830. *Phoradendron hexastichum* (DC.) Griseb. var. *ovatum* Stehlé, Bull. Soc. Bot. France **34:** 28. 1954, *nomen illegit.* TYPE: Cuba, Havana, 1825, *De la Ossa s.n.* (holotype, G-DC, IDC 800. 664: I. 4!).

Viscum cornifolium Presl, Epimel. Bot. 254. 1849. Included in *Phoradendron latifolium* Griseb. f. *hexasticha* Krug & Urban *in* Urban, Bot. Jahrb. Syst. **24:** 50. 1897. Although Urban placed this species in the synonymy of *P. latifolium* (= *P. piperoides*), it appears from the description and photo to be referable here. TYPE: Mexico, *Haenke s.n.* (holotype, PR, photo at ILL!).

Phoradendron hexastichum (DC.) Griseb. var. *longispica* Eichler *in* C. Martius, Fl. Brasil. **5**(2): 129. 1868. TYPE: "ad S. Gabriel de Cachoeira secundum Fl. Rio Negro, prov. do Alto Amazonas," *Spruce 2112* (holotype, hb. Delessert, G, photo at ILL!; isotypes, GH!, NY!, P!). Trelease erected a new species, *P. productipes* (TYPE: *Gardner 1676,* photo at ILL!), for this and other Brazilian members of *P. hexastichum.*

Phoradendron hexastachyum C. Wright *in* Sauvalle, Anales Acad. Ci. Méd. Habana 7: 345. 1870, *nomen nudum.* Sauvalle cited *C. Wright 1252.* This name is probably an error for *P. hexastichum.*

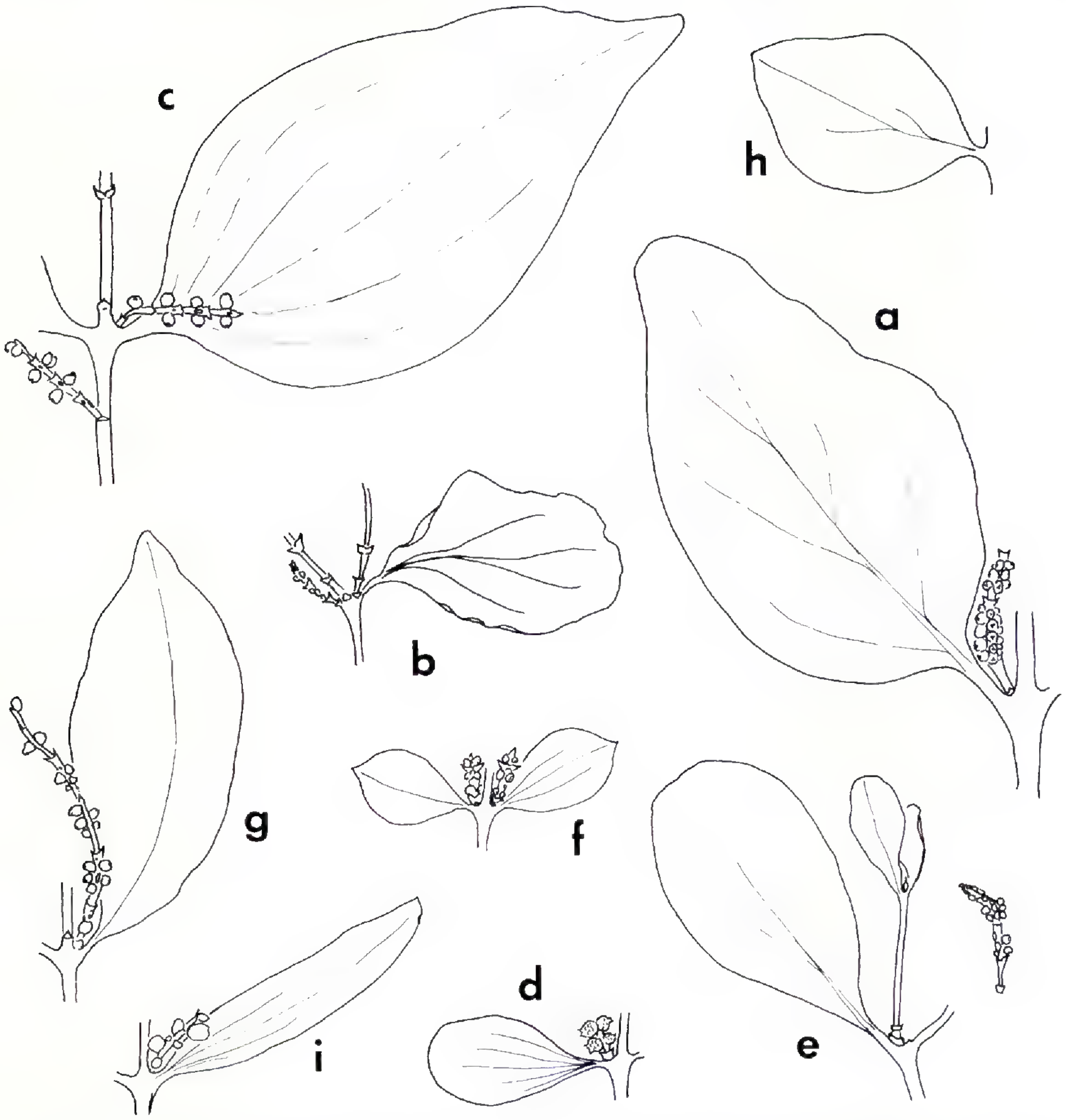

FIGURE 3. Leaves and inflorescences, × 0.53. a, *Phoradendron hexastichum, Wright 1252* (GH). b, *P. inequidentatum, Ayliffe, hb. Trin. 14320* (K). c, *P. martinicense, Beard 1132* (GH). d, *P. mucronatum, Fuertes 240* (A). e, *P. northropiae, Brace 5325* (GH). f, *P. ottonis, Britton & Freeman 2708* (GH). g, h, *P. piperoides*: g, *Howard & Proctor 14244* (A); h, *Sintenis 339* (GH). i, *P. quadrangulare, Heller 6186* (GH).

Phoradendron berterianum sensu Griseb. Fl. Brit. W. Indian Is. 313. 1860, *pro parte* (as to *Guilding s.n.*, St. Vincent, excluding synonyms).

Viscum verticillatum foemina Sieber, Pl. Mart. 227 (BM!, K!, P!). Not the specimen supposedly at G-DC, which is the type of *V. martinicense* DC.

Phoradendron hexastichum (DC.) Griseb. var. *angustifolium* Krug & Urban *in* Urban, Bot. Jahrb. Syst. **24:** 46. 1897. TYPE: Grenada, prope Plaisance in monte St. Catharine, 600 m alt., Dec. 1889, *Eggers 6140* (holotype, B, destroyed, photo at ILL!; isotypes, GH!, P!).

Phoradendron lapatanum Trel. Bull. Torrey Bot. Club **54:** 476. 1927. TYPE: Cuba, Península de Zapata, Santo Tomas, El Corte, 23 July 1920, *Roig & Cremata 2198* (holotype, NY!; fragment of holotype, ILL!).

Phoradendron stehlei Trel. *in* Stehlé, Bull. Soc. Bot. France **85:** 575, *nomen nudum*; *ibid.* **92:** 261. 1945. TYPE: Martinique, Calvaire du Gros-Morne aux Deux-choux, 4 September 1937, *Stehlé 2162* (holotype, ILL!). Isotypes at NY! and P! are *P. undulatum* (Pohl) Eichler; *Stehlé & Stehlé 2462* (P!) is labeled "co-typus" of *P. stehlei* but is *P. anceps*.

Stems strongly flattened, internodes dilated upward; cataphylls 1 (or 2) pair(s) at base of lateral branches only, separate, thick. Leaves with petiole 5–10 mm long; blade lanceolate to ovate, 5–12.2 × 2.2–8.5 cm, thick, apex and base rounded, base decurrent onto petiole, margin weakly revolute, nerves pinnate and prominent. Inflorescences 1 (or 2) per leaf axil, clavate, to 5 cm long, axis 1–2 mm thick when dry; cataphylls lacking (rarely 1 pair); bracts flaring, large, thick; fertile internodes up to 5, type 1b, obviously hexastichous, entirely pistillate, or staminate and pistillate flowers intermixed; if fertile internode bisexual, staminate flowers in separate vertical rank and internode sometimes > 6-ranked; flowers 6 to 10 per bract, mostly 1/2, but upper center 1 sometimes 2/1. Fruits globose, white; sepals closed.

DISTRIBUTION. Mexico, Venezuela, Brazil, Cuba, Hispaniola, Jamaica, Puerto Rico, Guadeloupe, Dominica, Martinique, St. Lucia, St. Vincent, Grenada.

Staminate individuals of *Phoradendron grisebachianum* may be confused with this species. See *P. grisebachianum* for discussion.

12. **Phoradendron inequidentatum** Rusby, Bull. Torrey Bot. Club **27:** 137. 1909. TYPE: Bolivia, Guanai, 2000 ft, May 1886, *Rusby 1544* (holotype, NY; isotype, GH!). FIGURE 3b.

Phoradendron jenmani Trel. Genus *Phoradendron,* 85. 1916. TYPE: British Guiana, Demerara, *Jenman 4678* (holotype, K, photo! in Trelease, 1916, *pl. 114b*). On p. 85, Trelease designated this specimen as the holotype; on p. 174, he listed *Jenman 2541* as the type and this specimen as a paratype.

Stems terete or only slightly compressed when young, monopodial or with branching bifurcate; cataphylls 1 to 3 pairs, first pair 2–3 mm above node, second 9–20 mm above first, separate to subannular, broadly ovate and flaring. Leaves with petiole 5–8 mm long; blade obovate, 4–7 × 2.3–5 cm, apex rounded to obscurely emarginate, base tapering, nerves basal. Inflorescences terminal or axillary, 1 or 2 per leaf axil, to 4 cm long, axis 2–3 mm thick when dry; cataphylls 1 or 2 pairs, flaring like bracts to form broad cup; fertile internodes 3 to 6; flowers 1 per bract or in triads (sometimes 3 flowers in 1 vertical rank), set in broad cup extending 0.3–0.5 mm up fruit; upper internodes pistillate, lower flowers of lower internodes staminate; most flowers 2/1, some 1/2. Fruits ovoid, yellow to red (*fide* Philcox, 1978); sepals erect.

DISTRIBUTION. Bolivia, Guyana, Trinidad.

Philcox (1978) listed this species as being from Trinidad and Guyana; however, Rusby's type is from Bolivia and appears more robust than the Trinidad specimens. Study of South American phoradendrons should clarify whether the distribution is indeed as discontinuous as it appears, if the two groups of

plants are separate taxa, or if they are connected by conspecifics currently masquerading under other names.

13. **Phoradendron martinicense** (DC.) Griseb. Fl. Brit. W. Indian Is. 314. 1860 (as to name only; Grisebach's description refers to *P. anceps*).
FIGURE 3C.

Viscum martinicense DC. Prodr. Syst. Nat. Regni Veg. **4:** 280. 1830. TYPE: Martinique, *Sieber 227, pro parte* (G-DC, photo not in microfiche). Type not seen, but the description is diagnostic. Other specimens of *Sieber 227* seen are *P. hexastichum.*

Stems terete; cataphylls 2 to 5 pairs between pairs of foliage leaves, first pair 1–5 mm distal to node, subsequent pairs 10–30 mm apart, small, generally distinct, on all axes. Leaves with petiole indistinct, 4–7 mm long; blade lanceolate to ovate, 5–17.7 × 2–8.8 cm, the apex acute to acuminate, ultimately obtuse, the base tapering, the nerves basal. Inflorescences 1 to 3 in axils of both leaves and cataphylls, to 6 cm long, axis ca. 1 mm thick when dry; cataphylls 1 to 3 pairs, like bracts flaring and navicular; fertile internodes 3 to 8 (to 11); in Lesser Antilles, flowers mostly in triads with uppermost flower staminate, lower 2 pistillate, sometimes 2 more pistillate flowers formed in 1a pattern, most pistillate flowers forming fruits so spikes tending to appear tetrastichous; in Trinidad, inflorescences type 1a, or occasionally type 1d, with 5 flowers per bract; flower orientation irregular but generally apical flower 1/2, lower ones 2/1. Fruits globose, yellow to orange, rough; sepals open.

DISTRIBUTION. Colombia, Venezuela, the Guianas, Peru, Guadeloupe, Dominica, Martinique, St. Lucia, Trinidad.

Phoradendron martinicense is distinguished from *P. crassifolium* on the basis of inflorescence morphology. At the northernmost limit of *P. martinicense,* in the Lesser Antilles, flowers are borne in triads or (rarely) five per bract in a 1a pattern. The 1a pattern becomes more common in Trinidad. North of the Amazon (Roraima, Pará, the Guianas, and parts of Venezuela and Colombia), plants with longer (more than ten flowers per internode) 1a inflorescences occur. Plants with triads (which are therefore more like *P. martinicense*) occur in Peru, Colombia, Venezuela, and Panama, mixed with plants with type 1a inflorescences. Plants from southern and eastern Brazil (Mato Grosso, Goiás, and southward) and Bolivia are more variable, with triads only on the upper internodes; the lower internodes are type 1b. The type of *P. crassifolium,* from southeastern Brazil, was drawn by Eichler with a type 1b inflorescence. The berries were drawn as smooth, whereas those of *P. martinicense* are roughwarty.

Other characters separating the two species are not reliable. Trelease (1916) claimed that plants of *Phoradendron martinicense* have shinier leaves than those of *P. crassifolium,* a character impossible to evaluate from herbarium specimens. He also said that *P. martinicense* has red fruits, while those of *P. crassifolium* are yellow. Most specimens of *P. martinicense* for which we have data have yellow to orange fruits, but labels on two specimens from Guyana at NY record the fruits as white; we have seen no record of red ones.

Phoradendron ayacuchanum Trel. ex J. F. Macbr. (Publ. Field Mus. Nat. Hist., Bot. Ser. **13:** 385. 1937) also appears to be part of this complex. The holotype (*Killip & Smith 22713,* ILL!) was collected in Peru and has a type 1a inflorescence.

This group is well-defined and would repay more careful investigation of the variability of the inflorescence type.

14. **Phoradendron mucronatum** (DC.) Krug & Urban *in* Urban, Bot. Jahrb. Syst. **24:** 34. 1897. FIGURE 3d.

Viscum mucronatum DC. Prodr. Syst. Nat. Regni Veg. **4:** 282. 1830. TYPE: Santo Domingo, *Bertero s.n.* (G-DC, IDC 800. 664: II. 1!).

Phoradendron emarginatum C. Martius *in* Eichler *in* C. Martius, Fl. Brasil. **5**(2): 118. *t. 38, fig. 1.* 1868. TYPE: in silvis Catingas prov. Minarum et Piauhy, 1839, *Claussen 252* (lectotype (Trelease, 1916), B, destroyed; isolectotype, hb. Delessert, G, photo at ILL!).

Phoradendron emarginatum C. Martius var. *minor* Eichler *in* C. Martius, *ibid.* 119. *Phoradendron minor* (Eichler) Trel. Genus *Phoradendron,* 117. 1916. TYPE: Brazil, inter Olho d'Agoa et Alegre, praedia prov. Piauhiensis, *M. Vaga s.n.* (holotype, B, destroyed; isotype, M, photo! in Trelease, 1916, *pl. 172*).

Phoradendron chaguaramasanum Trel. *in* Britton, Bull. Torrey Bot. Club **48:** 330. 1921. TYPE: Trinidad, Chaguaramas, *Britton 2718* (holotype, NY!; isotypes, GH!, K!).

Viscum myrtilloides sensu Sprengel, Syst. Veg. ed. 16 [17]. **1:** 488. [1824] 1825, *pro parte*; *Phoradendron myrtilloides* sensu Griseb. Fl. Brit. W. Indian Is. 314; not *V. myrtilloides* Willd. (see synonymy of *P. trinervium*).

Stems flattened but soon becoming terete, minutely glandular-papillate; internodes frequently < 2 cm long; cataphylls 1 pair at base of lateral branches only, separate or if fused then deeply cleft. Leaves with petiole indistinct; blade oblanceolate to obovate, 1.2–4.5 × 0.9–2.2 cm, the apex obtuse to truncate, sometimes apiculate, the base cuneate, the median nerve strong, 2 lateral basal nerves less prominent. Inflorescences generally solitary in leaf axils (rarely paired), much shorter than subtended internode, < 1.5 cm long, axis 1–3 mm thick when dry; prophylls prominent; cataphylls absent; bracts fused, broadly ovate; fertile internodes 2 to 4; flowers in triads, upper 1 staminate and lower 2 pistillate, most of latter producing fruit so that fruiting inflorescence appears tetrastichous; apical flower 2/1, lower ones 1/2. Fruits globose, white to orange, pericarp prominently warty; sepals erect.

DISTRIBUTION. Panama, Venezuela, Brazil, Hispaniola, Antigua, Guadeloupe, Dominica, Martinique, Trinidad.

15. **Phoradendron northropiae** Urban *in* Northrop, Mem. Torrey Bot. Club **12:** 33. *pl. 4.* 1902. TYPE: Bahamas, Andros Island, Conch Sound, 1890, *Northrop & Northrop 551* (lectotype (Gillis, 1976), F, not seen; isolectotypes, GH!, K!, NY!). FIGURE 3e.

Stems flattened, rapidly becoming terete; branching mostly bifurcate; cataphylls 1 pair near base of lateral branches only, appearing truncate on older specimens. Leaves with petiolar region short; blade oblanceolate to obovate (rarely obcordate), 3–6(–9) × 1.7–4(–6) cm, the apex rounded, truncate, or

emarginate, the base tapering, the nerves pinnate, obscure. Inflorescences 1 to 3 per leaf axil, to 3.5 cm long, axis ca. 2 mm thick when dry; cataphylls generally 1 pair, these and bracts partially or wholly fused, flaring-ovate, white margined; fertile internodes up to 5, type 1a; flowers 5 to 11 per bract, upper one(s) staminate, lower ones pistillate; apical flower 2/1, lower ones 1/2. Young fruits globose, golden, mature fruits white(?) to red; sepals erect. (Fruit color *fide* Correll & Correll, 1982.)

DISTRIBUTION. Bahamas.

Gillis (1976) merged this with *Phoradendron racemosum,* but Correll and Correll (1982) maintained the two species as distinct because of the difference in fruit color. Our specimens have no data on fruit color, but *P. northropiae* is distinctive in having consistently smaller leaves that are never acute but frequently emarginate at the apex. Rizzini (1978) reported this species from Venezuela and Brazil. See also discussion under *P. racemosum* and *P. inequidentatum,* which may be related.

16. **Phoradendron ottonis** Eichler *in* C. Martius, Fl. Brasil. **5**(2): 119. 1868. TYPE: Venezuela, Orituca, *Otto 565* (holotype, B, destroyed).

FIGURE 3f.

Phoradendron caerulescens Trel. *in* Britton, Bull. Torrey Bot. Club **48:** 330. 1921. TYPE: Trinidad, Chacachacare Island, 13 April 1920, *Britton & Hazen 1726* (holotype, NY!; isotype, GH!).

Stems flattened and 2-winged to more or less rhombic; internodes often only 1–2 cm long, flaring above; cataphylls 1 or 2 pairs, on lateral branches only, immediately above node, not strongly spreading, more or less deltate. Leaves with petiole indistinct; blade ovate, elliptic, or suborbicular, 1.4–3 × 1.1–2.1 cm, glaucous, the apex obtuse to acute, mucronate, the base cuneate, the nerves basal, finely reticulate. Inflorescences solitary in leaf axils, shorter than internode they subtend, to 1.4 cm long, axis 1–2 mm thick when dry; prophylls large and obvious, cataphylls lacking; bracts broadly navicular, erose margined; fertile internodes 2 to 4; flowers in triads; apical flowers 2/1, lower ones 1/2 or irregular. Fruits ovoid, warty; sepals erect, open.

DISTRIBUTION. Trinidad, Venezuela.

This species is very similar to *Phoradendron mucronatum,* from which it is distinguished by its suborbicular, glaucous leaves.

17. **Phoradendron piperoides** (Kunth) Trel. Genus *Phoradendron,* 145. 1916.

FIGURE 3g, h.

Loranthus piperoides Kunth *in* Humb., Bonpl., & Kunth, Nova Gen. Sp. Pl. **3:** 443. 1818. *Viscum piperoides* (Kunth) DC. Prodr. Syst. Nat. Regni Veg. **4:** 281. 1830. TYPE: Colombia, Papayan, 1871, *Bonpland s.n.* (P-HBK!; IDC 6209-2. 88: III. 6!).
Viscum latifolium Sw. Fl. Ind. Occ. **1:** 268. 1797. *Phoradendron latifolium* (Sw.) Griseb. Fl. Brit. W. Indian Is. 314. 1860, excluding synonyms of Macfadyen, *V. flavens*; not

Lam. 1789. TYPE: "habitat in arboribus Jamaicae," *Swartz s.n.* (holotype, S, not seen).

Viscum schottii Pohl *in* DC. Prodr. Syst. Nat. Regni Veg. **4:** 281. 1830. *Phoradendron schottii* (Pohl) A. Gray, U. S. Expl. Exped., Phan. **15:** 742. 1854. TYPE: Brazil, "on the Organ Mountains," 1828, *Pohl s.n.* (holotype, G-DC, IDC 800. 663: III. 4!). Trelease (1916, p. 147) cited *Pohl 4319* as the type, but on p. 184 listed the type as *Pohl 246,* PR (photos!, *plate 217* and ILL).

Viscum tereticaule DC. Prodr. Syst. Nat. Regni Veg. **4:** 280. 1830. *Viscum teretifolium* "DC." *in* Hemsley, Biol. Centr.-Amer., Bot. **3:** 85. 1882, probably an error for *tereticaule.* "*Phoradendron tereticaule,*" Index Kew. **3:** 503. 1894, not Lam. 1789.

Viscum tereticaule DC. var. *cubense* DC. Prodr. Syst. Nat. Regni Veg. **4:** 280. 1830. TYPE: Cuba, *De la Ossa s.n.* (G-DC, IDC 800. 663: II. 4, 5!).

Viscum fockeanum Miq. Linnaea **18:** 60. 1844, from description. TYPE: "species ut videtur Surinami in Citris aurantis vulgaris . . . ," *Focke s.n.* (holotype, L or U, not seen).

Viscum laurifolium Presl, Epimel. Bot. 255. 1849. *Phoradendron laurifolium* (Presl) Eichler *in* C. Martius, Fl. Brasil. **5**(2): 107. 1868. TYPE: Mexico, "in regione temperata," *Leibold s.n.* (holotype, PR, photo at ILL!).

Phoradendron biolleyi K. Krause, Notizbl. Königl. Bot. Gart. Berlin **5:** 264. 1912, *fide* Burger, Fieldiana Bot. **13:** 75. 1983. TYPE: Costa Rica, San Mateo, 1892, *Biolley 7078* (holotype, B, destroyed).

Phoradendron piperoides (Kunth) Trel. f. *composita* Trel. Genus *Phoradendron,* 148. 1916. TYPE: Brazil, Rio de Janeiro, *Ule 4800* (holotype, B, destroyed).

Phoradendron ficulneum Trel. Repert. Spec. Nov. Regni Veg. **25:** 55. 1928. TYPE: Haiti, La Selle, Pétionville, Tête de l'Eau, 500 m, *Ekman 9370* (location of holotype not cited, no specimen at ILL; isotype, K!).

Stems terete; cataphylls 1 pair on percurrent axes, 3–6 mm above node, generally 2 pairs on lateral branches, 1 pair just above node, the other 1–2 cm above first, separate, triangular, grayish. Leaves with petiole ≤ 5 mm long; blade elliptic to lanceolate, appearing distichous because of interspersed cataphylls, 3–10 × 1.2–4.1 cm, apex acuminate, base cuneate, nerves pinnate and obscure. Inflorescences 1 to 5 per leaf axil, standing erect on fresh specimens, to 5(–7) cm long, axis 1–2 mm thick when dry; cataphylls usually 1 or 2 pairs, crateriform like bracts; fertile internodes up to 7, type 1a or sometimes triads; flowers 3 to 5 per bract, staminate and pistillate intermixed in same internode; apical flower 2/1, lower ones 1/2. Fruits ovoid, yellow to orange, drying wrinkled; sepals stiffly erect.

DISTRIBUTION. Mexico to Argentina, Hispaniola, Cuba, Jamaica, Puerto Rico, St. Bart's (Wikström, 1826), Guadeloupe, Dominica, Martinique, St. Lucia, St. Vincent, Grenada, Trinidad, Tobago.

This species is well named; the upright stance of the inflorescences and the apparently distichous phyllotaxy make it look from a distance like a species of *Piper.*

Phoradendron ficulneum is the name given to the round-leaved forms of *P. piperoides.* The two leaf shapes fully intergrade (see FIGURE 3g, h).

18. **Phoradendron quadrangulare** (Kunth) Griseb. Fl. Brit. W. Indian Is. 711. 1864 (as to name only—Grisebach cited a Crueger specimen from Trinidad, which is *P. trinervium*). FIGURE 3i.

Loranthus quadrangularis Kunth *in* Humb., Bonpl., & Kunth, Nova Gen. Sp. Pl. **3:** 444. 1818. *Viscum quadrangulare* (Kunth) DC. Prodr. Syst. Nat. Regni Veg. **4:** 283. 1830. TYPE: "regni Novo-Granatensis, prope Pandi et Fusagasuga, alt. 940 h.," *Bonpland s.n.* (holotype, P-HBK!; IDC 6209-2. 89: I. 2!).

Viscum angustifolium Bertero ex Sprengel, Syst. Veg. ed. 16 [17]. **1:** 487. [1824] 1825, *fide* Urban (1897); not *Loranthus angustifolius* Kunth, 1818, or *Phoradendron angustifolium* Eichler, 1868. LECTOTYPE (Trelease, 1916): Portorico, *Bertero 1234* (B, destroyed).

Viscum trigonum D. Dietr. Syn. Pl. **1:** 546. 1839, *pro parte* (excluding synonym *Loranthus sessilis* H. Balbis), *fide* Urban (1897). TYPE: "ad sylvas maritimas Portorici et Guadelupae 1. *Bertero* [*s.n.*]" (JE, not seen). See also *Phoradendron trinervium.*

Viscum tetragonum A. Rich. Hist. Phys. Pol. Nat. Cuba, Pl. Vasc. 647. 1845, not DC. 1830, or *Phoradendron tetragonum* Ule, 1915. TYPE: Cuba, *Sagra s.n.*, hb. Richard (P!). See also *P. trinervium.*

Viscum randiae Bello, Apuntes Fl. Puerto-Rico, 278. 1881. *Phoradendron randiae* (Bello) Britton, Bot. Porto Rico **5:** 257. 1924, *fide* Urban (1897). TYPE: "en el cerro de la mesa, Mayagues," *Bello s.n.* (holotype, B, destroyed).

Phoradendron antillarum Trel. Genus *Phoradendron,* 111. 1916. TYPE: Cuba, *Wright 1302* (holotype, n.v., photo at ILL!; isotypes, GH!, K!, NY!, P!). Trelease did not record where he photographed the holotype; the specimen in the photograph is not the one at GH or NY. Wright's Cuban specimens were widely distributed, and the photograph might have been taken at B.

Phoradendron antillarum Trel. var. *orientalis* Trel. *ibid.* 112. TYPE: eastern Cuba, Guantanamo Bay, 17–30 March 1909, *Britton 2119* (holotype, NY!, photo at ILL!).

Phoradendron antillarum Trel. var. *orientalis* Trel. f. *longa* Trel. *ibid.* TYPE: Cuba, Camaguey to Santayana, 4 April 1909, *Britton 2415* (holotype, NY!, photo at ILL!).

Phoradendron venezuelense Trel. *ibid.* 111. TYPE: Venezuela, Tovar, *Fendler 1810* (holotype, K, photo at ILL!; isotype, GH!).

Phoradendron moringicola Trel. Repert. Spec. Nov. Regni Veg. **26:** 343. 1929. TYPE: Haiti, Monfleury on Moringa, 27 October 1927, *Ekman 9180* (holotype, ILL!; isotype, A!).

Phoradendron rubrum sensu Griseb. Fl. Brit. W. Indian Is. 314. 1860, and other authors, not L.

Stems flattened to more or less rhombic when young; cataphylls 1 pair at base of lateral branches only, small, annular, scarcely spreading. Leaves with petiole indistinct; blade linear, oblong to more or less oblanceolate, 3–9(–13) × 0.4–1.8(–2.5) cm, ca. 5 times longer than wide, the apex acute to obtuse, sometimes apiculate, the base tapering, the nerves basal, obscure. Inflorescences 1 to 3 per leaf axil, 2–2.5(–5) cm long, axis ≤ 1 mm thick when dry; cataphylls lacking (occasionally 1 pair on some branches); bracts small, fused, collarlike; fertile internodes up to 5, type 1a[2], flowers 7 to 9 (to 12) per bract, not deeply sunken in rachis, staminate and pistillate intermixed or pistillate only; apical flowers 2/1, lower ones 1/2, but orientation not wholly consistent. Young fruits oblong with golden sheen; mature fruits globose, bright yellow; sepals closed.

DISTRIBUTION. Guatemala, Costa Rica, Panama, Ecuador, Peru, Colombia, Venezuela, Argentina, Cuba, Hispaniola, Jamaica, Puerto Rico, Bahamas, Antigua (Trelease, 1916, *Nicholson 16*), Guadeloupe (Urban, 1897, *Bertero*

[2] *Winters 562* (GH) is type 1b.

s.n., the type of *Viscum trigonum*; Stehlé, 1954, *Sprengel s.n.*), St. Vincent (Grisebach, 1860, *Guilding s.n.*), Trinidad.

Phoradendron quadrangulare has smooth to wrinkled fruits with closed sepals, as well as type 1a inflorescences and small, narrow leaves. It can thus be easily distinguished from *P. gracile,* which has warty fruits, from *P. rubrum,* which has erect sepals, and from *P. haitense* and *P. hartii,* both of which have larger leaves and at least some type 1d or 1e inflorescences.

The holotype of *Phoradendron moringicola* has unusually large (10–13 cm) leaves, but in all other respects it agrees with this species. The isotype at A is more nearly typical, with leaves 4–9 cm long.

Krug and Urban's (*in* Urban, 1897) species description is based on Antillean specimens; in South American plants spikes can be up to 5 cm long with seven fertile internodes. The holotype of *Loranthus quadrangularis* at P has leaves measuring 5–6 × 1.5 cm that are somewhat more lanceolate than those of Antillean plants, spikes 3.4–4 cm long with four or five fertile internodes, and 11 to 13 flowers per bract. Krug and Urban (*in* Urban, *ibid.*) reported that all flowers on this specimen are pistillate. Plants with spikes as large as those of the type are uncommon in both South America and the Greater Antilles.

Trelease (1916) claimed that the epithet *quadrangulare* should be applied only to South American plants because of the larger spikes on the type. Based on the range of variation in both South American and Antillean specimens, there seems no rationale for placing them in separate species. If, however, it is decided that they are different, then the earliest Caribbean name is *Phoradendron randiae.*

It is not clear where Trelease obtained his information on fruit color—he recorded white for *Phoradendron quadrangulare,* whereas label data on all specimens we have seen indicate that the fruits are yellow to orange. This is confirmed by the field observations of Wiens (pers. comm.), who has seen the species in both Ecuador and Mexico. He also notes that the species is common in seasonally dry coastal habitats.

Rizzini (1978) suggested uniting *Phoradendron quadrangulare* and *P. rubrum* because the Venezuelan material has orange to red fruits and semierect sepals, supposedly intermediate characters. He also claimed that the number of flowers per internode, leaf size, and leaf shape are approximately the same in both species. We have found that the two species are easily distinguished in the Caribbean by the red-orange to scarlet fruits, flattened stems, broad leaves, and open sepals of *P. rubrum* vs. the yellow to orange fruits, quadrangular stems, narrow leaves, and closed sepals of *P. quadrangulare.* Part of the confusion may be attributed to Grisebach's misapplication of the name *P. rubrum.*

19. **Phoradendron racemosum** (Aublet) Krug & Urban *in* Urban, Bot. Jahrb. Syst. **24:** 46. 1897. FIGURE 4a.

Viscum racemosum Aublet, Hist. Pl. Guiane Fr. **2:** 895. 1775. LECTOTYPE (Gillis, 1976): Guiana (P, specimen not found).

Viscum macrophyllum Sprengel, Syst. Veg. ed. 16 [17]. **1:** 488. [1824] 1825; not DC. 1830, Macfad. 1850, or *Phoradendron macrophyllum* Ule, 1915. TYPE: Porto Rico, 1820, *Bertero s.n.* (holotype, B, destroyed; isotype, G-DC, IDC 800. 664: I. 6!).

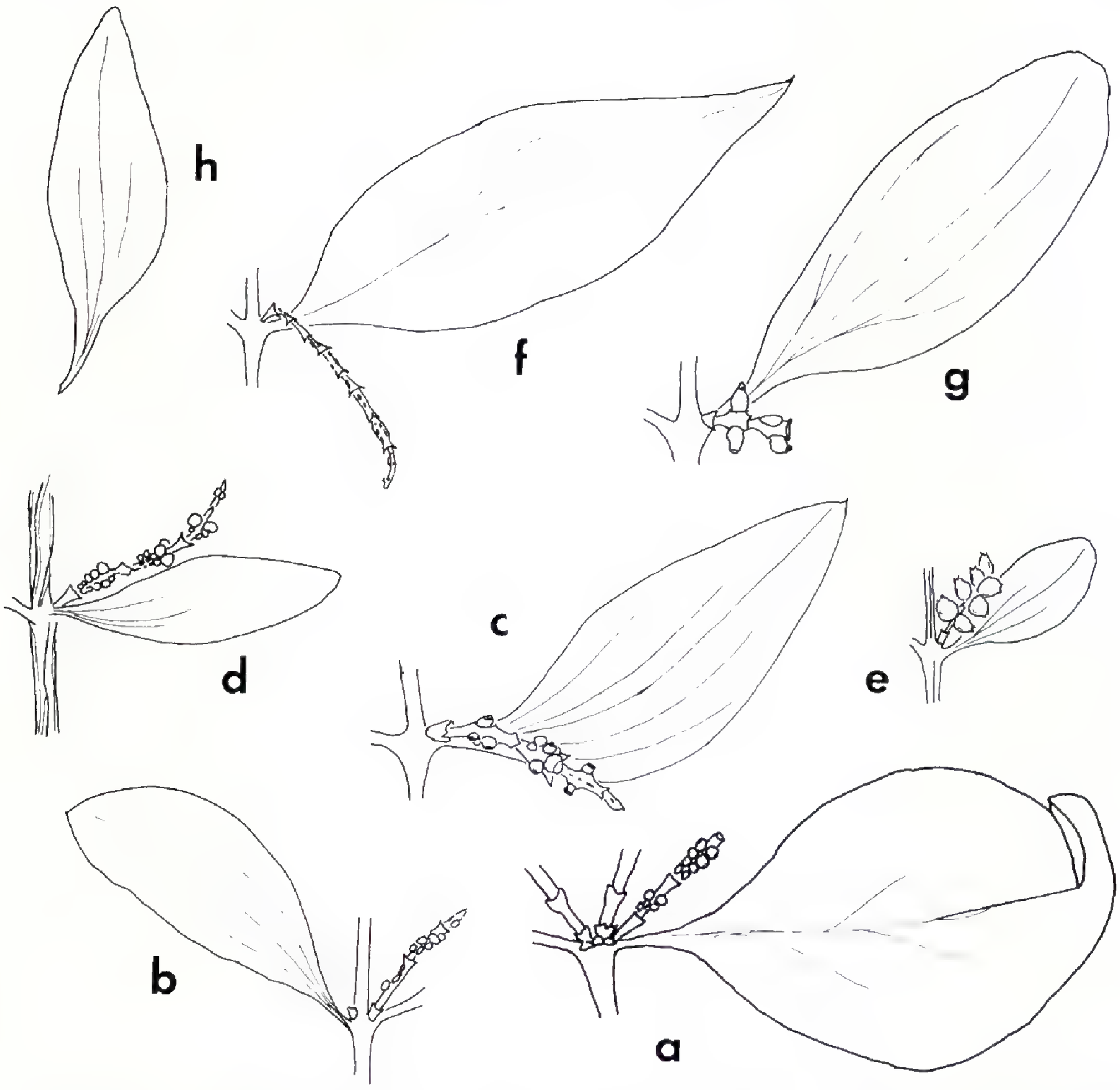

FIGURE 4. Leaves and inflorescences, × 0.53. a, *Phoradendron racemosum, Sintenis s.n.*, 1/86 (GH). b, *P. rubrum, Britton & Millspaugh 5867* (NY). c, *P. solandrae, Proctor 37603* (A). d, *P. tetrapterum, Proctor 15680* (A). e, *P. trinervium, Correll 43845* (GH). f, *P. undulatum, anon. s.n.* (GH). g, h, *P. wattii*: g, *Proctor 27631* (GH); h, *Maxon & Killip 1055* (A).

Viscum glandulosum Miq. Linnaea **18:** 60. 1844. *Phoradendron glandulosum* (Miq.) Eichler *in* C. Martius, Fl. Brasil. **5**(2): 134m. 1868. TYPE: Surinam, *Focke s.n.* (holotype, U; photo! of possible isotype at K).

Phoradendron pennivenium Eichler *in* C. Martius, *ibid.* 128. *t. 42* (excluding synonyms of De Candolle); not *Viscum pennivenium* DC. (TYPE: French Guiana, 1820, *Perrottet s.n.*, G-DC, IDC 800. 664: II. 2!, which is a species of *Oryctanthus*). SYNTYPES: *Spruce 185, 733, 788*; *Hostman 729*; *Wullschlägel s.n.*; *Schomburgk 554* (all at B, destroyed). Eichler's figure clearly agrees with *P. racemosum*.

Stems flattened but soon becoming terete; branches often bifurcate; cataphylls generally 2 pairs on lateral branches only, 1 pair just above node, second pair less than 1 cm above first, large, flaplike or somewhat fused. Leaves with petiole 8–15 mm long; blade ovate to nearly orbicular, 5–14 × 2.9–10 cm, thick, the apex subacute, obtuse, or rounded, the base rounded and tapering, the margin occasionally somewhat revolute, the nerves pinnate. Inflorescences terminal or

axillary, often appearing in dense clusters of up to 15, to 6 cm long, axis 2–4 mm thick when dry; cataphylls 1 pair, thick and flaring like bracts; fertile internodes generally 4 or 5 (or 6), type 1a; flowers 7 to 9 (to 11) per bract, apical one staminate, lower ones pistillate; apical flower 2/1, lower ones 1/2. Fruits ovoid, white; sepals erect.

DISTRIBUTION. Venezuela, Surinam, Brazil, Cuba, Hispaniola, Puerto Rico, Bahamas, St. Croix, Trinidad.

This species is similar to *Phoradendron hexastichum,* but the inflorescence is type 1a, the leaves are more nearly orbicular, and branching is bifurcate. Two specimens at K from Trinidad, *Baker 14593* and *Ayliffe 16499,* are apparently referable to this species, but most leaves of both are obovate and emarginate. The largest leaf of *Ayliffe 16499* is only 6 cm long, and the specimen appears similar to *P. northropiae,* a species endemic to the Bahamas. Also at K is *Smith 2967,* from the Brazil-Guyana boundary, which resembles the Ayliffe specimen. *Phoradendron racemosum* and the similar *P. northropiae* may be part of a much more widespread group that may also include *P. inequidentatum.*

20. **Phoradendron rubrum** (L.) Griseb. Fl. Brit. W. Indian Is. 314. 1860 (as to name only—*P. rubrum* sensu Griseb. = *P. quadrangulare*). FIGURE 4b.

Viscum rubrum L. Sp. Pl. 1023. 1753, not Sprengel, [1824] 1825. LECTOTYPE (Dandy, 1958): Catesby, Nat. Hist. Carolina **2:** *pl. 81.* 1743. TYPOTYPE (Gillis, 1976): BM!, Herb. Sloane 232: 2 (initialed R.H.S.), 8 (initialed R.H.D., lectotype), 16 (not initialed). No specimen in LINN. See also Howard & Staples (1983).

Phoradendron tetrastachyum Griseb. var. *spathulifolium* Griseb. Catal. Pl. Cubens. 120. 1866. *Phoradendron spathulifolium* (Griseb.) Krug & Urban *in* Urban, Bot. Jahrb. Syst. **24:** 41. 1897. TYPE: *Wright 1300b* (holotype, GOET, not found; isotype, GH!).

Stems flattened to obscurely rhombic but not quadrangular, becoming terete; internodes often < 3 cm; cataphylls generally 1 pair on lateral branches only, 1–2 mm distal to node, separate or only slightly fused. Leaves with petiole indistinct; blade elliptic to oblanceolate, 2.4–7.5 × 0.9–3 cm, the apex obtuse to rounded, the base tapering, the nerves basal, obscure to prominent. Inflorescences up to 2 per leaf axil, occasionally branching, to 5 cm long, axis ca. 1 mm thick when dry; prophylls deltate, cataphylls 0 (or 1) pair(s); bracts not at all separate, forming infundibular cup; fertile internodes 2 to 4, commonly type 1a or 1d, rarely triads; flowers 3 to 9 per bract, staminate and pistillate intermixed; apical flower 2/1, lower ones 1/2. Fruits globose, red-orange to scarlet; sepals triangular, erect.

DISTRIBUTION. Cuba, Bahamas, Cayman Islands.

The *Phoradendron rubrum* complex is a group of one to six species characterized by erect sepals, cataphylls on lateral branches only, inflorescences triads or type 1a, and pistillate or mixed spikes. The leaves are consistently obovate to oblanceolate, with basal nervation, but vary from 2 to 7.5 cm in length. Variation in other characters appears to have a geographic basis. In this

group we recognize two species, *P. rubrum* and *P. trinervium,* but the latter appears to comprise at least five poorly delimited entities (see *P. trinervium* for more detailed discussion of these). *Phoradendron rubrum* is most easily distinguished from *P. trinervium* by its flattened stem, its frequently longer leaves, and its scarlet fruits. It is often parasitic on *Swietenia mahogani* (L.) Jacq.

The complex is distributed throughout the West Indies, although it is curiously rare on Hispaniola. *Phoradendron rubrum* occurs in Cuba, the Bahamas, and the Cayman Islands. The Cuban specimens of *P. rubrum* are frequently difficult to distinguish from *P. gundlachii* Krug & Urban, apparently a Cuban endemic with white fruits and closed sepals; *P. gundlachii* may not be at all closely related to the rest of *P. rubrum,* but it looks similar when mature fruits are absent. Cooley (1963) has reported this species from Key Largo, Florida, but a search several years later (Wiens, pers. comm.) failed to re-locate it.

21. **Phoradendron solandrae** Proctor, J. Arnold Arbor. **63:** 228. 1982. TYPE: Jamaica, Clarendon Parish, Knox Woodland, ca. 1.3 mi due southeast of Spaldings P.O., alt. 2800–3000 ft, 19 November 1977, *Proctor 37430* (holotype, IJ; isotype, A!). FIGURE 4c.

Stems flattened, becoming terete; cataphylls 1 pair, at base of lateral branches only, separate or only partially fused, spreading, broadly ovate, white margined. Leaves with petiole 5–10 mm long; blade lanceolate, oblong, or elliptic, falcate, 5–12(–15) × 1.4–3(–5) cm, apex tapering but ultimately obtuse, base cuneate, nerves predominantly basal. Inflorescences 1 to 3 (to 6) per leaf axil, fleshy, clavate, to 5 cm long, drying yellow-brown with axis 1–3 mm thick; cataphylls lacking or 1 pair, entire to 3-lobed, flaring infundibular, white margined; bracts more nearly fused, also flaring and infundibular; fertile internodes 2 to 4, type 1a or triads; flowers 3 to 5 per bract, sunken in large cupules, terminal joint staminate, others pistillate; apical flower generally 2/1, sometimes 1/2, the lower ones 1/2, sometimes 2/1. Fruits globose, orange; sepals closed.

DISTRIBUTION. Endemic to Jamaica.

This species is similar to *Phoradendron barahonae,* from which it is distinguished by its fewer flowers per internode, its prominent cupules around each fruit, and its characteristic yellow color on drying.

22. **Phoradendron tetrapterum** Krug & Urban *in* Urban, Bot. Jahrb. Syst. **24:** 35. 1897. TYPE: Jamaica, between Hope and Grove, 267 m, 4 August 1896, *Harris 6393* (lectotype (Trelease, 1916), B, destroyed; isolectotype, NY!). FIGURE 4d.

Phoradendron multifoveolatum sensu Kuntze, Rev. Gen. Pl. **2:** 587. 1891, *fide* Urban (1897); not Eichler, 1868.

Stems obviously 4-angled and winged; cataphylls 1 pair on lateral branches only, 1–2 mm above node, thick and flaring, annular, bifid. Leaves with petiole 4–10 mm long, clasping stem; blade variable, lanceolate to elliptic to broadly

oblanceolate, 2.6–10.3 × 1.1–2.1(–3) cm, the apex acute to rounded, apiculate, the base tapering, the nerves basal to subbasal. Inflorescences 1 to 3 per leaf axil, to 7.5 cm long, axis 1–2 mm thick when dry; cataphylls lacking (occasionally 1 pair), like bracts fused and navicular; fertile internodes up to 6, type 1a; up to 15 flowers per bract; apical flower 2/1, lower ones 1/2. Fruits globose, white; sepals closed but not meeting.

DISTRIBUTION. Cuba, Hispaniola, Jamaica, Puerto Rico, Martinique (Urban, 1897, *Isert s.n.*, 1787, hb. Haun), St. Vincent, Trinidad.

Krug and Urban (*in* Urban, 1897) described this as distinct from *Phoradendron multifoveolatum* Eichler and *P. crulsii* Urban, both of which have six-seriate inflorescences, and *P. tovarense* Urban, which is eight- to ten-seriate. Kuijt (pers. comm.) suggests that *P. tetrapterum* is synonymous with *P. dipterum* Eichler. Resolution of these questions will require detailed study of the South American phoradendrons.

Phoradendron tetrapterum is reported to grow exclusively on other mistletoes.

23. **Phoradendron trinervium** (Lam.) Griseb. Fl. Brit. W. Indian Is. 314. 1860. FIGURE 4e.

Viscum trinervium Lam. Encycl. Méth. Bot. **3:** 57. 1789; not Sprengel, [1824] 1825. LECTOTYPE (Trelease, 1916): Martinique, "près de Fort Royal," 1787, *Isert s.n.* (P-LAM!; IDC 6207-15. 578: III. 4!, 7!).

Viscum myrtilloides Willd. Sp. Pl. ed. 4. **2:** 739. 1806. *Dendrophthora myrtilloides* (Willd.) Rolfe, Bull. Misc. Inform. **81:** 274. 1893. *Phoradendron myrtilloides* (Willd.) Griseb. Mem. Amer. Acad. Arts **8:** 191. 1861. TYPE: "habitat in Martinicae," hb. Willd. no. 18296 (IDC 7440. 1330: II. 9!). Type not as suggested by Kuijt (1961), *Isert s.n.* (P-LAM), the same specimen as the lectotype of *V. trinervium.*

Loranthus domingensis Ham. Prodr. Pl. Indiae Occ. 33. 1825. *Phthirusa domingensis* (Ham.) Eichler *in* C. Martius, Fl. Brasil. **5**(2): 134i. 1868. *Dendropemon domingensis* (Ham.) Tieghem, Bull. Soc. Bot. France **42:** 1170. 1895. *Phoradendron trinervium* (Lam.) Griseb. var. *domingense* (Ham.) Krug & Urban *in* Urban, Bot. Jahrb. Syst. **24:** 38. 1897. *Phoradendron domingense* (Ham.) Trel. Genus *Phoradendron,* 102. 1916. TYPE: Hispaniola, hb. Desvaux. No specimen found at P. Urban (1920) cited the type as "Hb. Desv. (nunc Paris).—Jamaica."

Viscum tetragonum DC. Prodr. Syst. Nat. Regni Veg. **4:** 282. 1830; not A. Rich. 1845, or *P. tetragonum* Ule, 1915. TYPE: in sylvis maritimis Porto Rico, February 1820, *Bertero s.n.* (holotype, G-DC, IDC 800. 664: I. 8!). See also *Phoradendron quadrangulare.*

Viscum oblongifolium DC. *ibid.* 283. *Phoradendron oblongifolium* (DC.) Eichler *in* C. Martius, Fl. Brasil. **5**(2): 134m. 1868. TYPE: "montagnes de la Guadeloupe le 20 juin, 1824," *Perrottet s.n.* (holotype, G-DC, IDC 800. 664: II. 3, 4!).

Viscum trigonum D. Dietr. Syn. Pl. **1:** 546. 1839, *pro parte, fide* Urban (1897). See also *Phoradendron quadrangulare.*

Viscum jamaicense Macfad. Fl. Jamaica **2:** 195. 1850. TYPE: Jamaica, Port Royal Mountains, *Macfadyen s.n.* (K!).

Phoradendron quadrangulare sensu Griseb. Fl. Brit. W. Indian Is. 711. 1864, *fide* Urban (1897).

Phoradendron rubrum var. *brevispica* Eichler *in* C. Martius, Fl. Brasil. **5**(2): 121. 1868 (excluding synonym *Viscum mucronatum* DC. and location Santo Domingo).

SYNTYPES: "in insulis Martinica, Antigua, Porto Rico et S. Domingo; *Bertero s.n., Wullschlägel s.n., Isert s.n.* (*Hb. Willd. 18296*)." (IDC 7440. 1330: II. 9! = type of *P. trinervium* and *P. myrtilloides*.)

Phoradendron rubrum var. *latifolia* Eichler *in* C. Martius, *ibid., fide* Urban (1897). TYPE: in Antigua insula, *Wullschlägel s.n.* (holotype, B, destroyed).

Viscum rubrum sensu Sprengel, Syst. Veg. ed. 16 [17]. **1:** 488. [1824] 1825, and other authors, not L.

Phoradendron verticillatum sensu Fawcett & Rendle, Fl. Jamaica **3:** 96. 1914, not Druce, 1914. *Viscum verticillatum* Mayc. Fl. Barbadensis 384. 1830, not L. 1753.

Stems quadrangular, becoming terete; internodes often < 3 cm; cataphylls generally 1 pair, on lateral branches only, 1–2 mm distal to node, partially fused, white edged. Leaves with petiole indistinct; blade elliptic, obovate, or oblanceolate, widest at or above middle, 1.5–6 × 0.8–2.7(–3.2) cm, the apex truncate, obtuse, or rounded, occasionally minutely apiculate, the base tapering, the nerves basal, obscure. Inflorescences 1 (or 2) per leaf axil, to 5 cm long, generally shorter than subtended internode, axis ≤ 1 mm thick when dry; prophylls triangular, caducous; cataphylls 0 (or 1) pair(s), like bracts 3-lobed or nearly entire, partially fused, often notched at joint, and white margined; fertile internodes 2 to 4, in some specimens flowers only in upper half of internode, mostly in triads or varying within same plant to type 1a, or single pistillate flower per bract, or (rarely) type 1d; flowers 3 to 5 (to 7) per bract; internodes wholly pistillate, wholly staminate, or staminate and pistillate flowers intermixed; flower orientation variable. Fruits globose, yellow to orange or red-orange; smooth, or with ring of obscure papillae or warts near base of sepals around top of fruit, sepals triangular, erect.

DISTRIBUTION. Costa Rica, Panama, Venezuela, Jamaica, Cayman Islands, Hispaniola, Puerto Rico, Bahamas, Anguilla, St. Martin, St. Bart's, Antigua, Saba, St. Eustatius, Montserrat, Guadeloupe, La Désirade, Dominica, Martinique, St. Lucia, St. Vincent, the Grenadines, Barbados (Maycock, 1830; Fawcett & Rendle, 1914), Trinidad, Tobago, Curaçao, Margarita.

Although some authors have referred these plants to *Viscum verticillatum* L., Fawcett and Rendle (1914) claimed that Linnaeus's descriptions of *V. verticillatum* are based on diseased and monstrous specimens of *Cissus* sp. (LINN 1166.10). Nicolson and Jarvis (1984) have confirmed this fact and have formally transferred the epithet to *Cissus*.

According to Urban (1897), the Venezuelan record of *Phoradendron trinervium* in Grisebach (1860) is *Fendler 1809* and is referable to *P. mucronatum*.

This species is very similar to *Phoradendron rubrum, q.v.* As defined here, *P. trinervium* includes five poorly delimited entities. The first group is characterized by oblanceolate leaves somewhat longer than in *P. trinervium* sensu stricto and inflorescences somewhat longer than in other members of the species. The uppermost internode of the inflorescence has one pistillate flower per bract, while the lower internodes are either wholly pistillate, wholly staminate, or mixed—with the upper flower staminate and the lower two pistillate. Plants in this group tend to have flowers borne in the upper half of the internode only, giving the inflorescence an elongate appearance. This form is the predominant one on Jamaica, but we have also found it (although less frequently) in the

Bahamas and Lesser Antilles. Where fruit color has been recorded, it is described as yellow to orange. The fruits often have a ring of obscure warts or papillae around the top just below the sepals. (These are often hidden by the wrinkling of dried fruits and are therefore only consistently visible when the fruits are boiled.)

Some authors have referred to these plants as *Phoradendron domingense* (Ham.) Trel., a name for which we have been unable to find the type. (Types for most of Hamilton's species are said to be in Paris, but many have not been located (Howard *et al.*, 1981)). The protolog of *P. domingense* cites the specimen as coming from Hispaniola, although Urban (1920) later claimed that it was from Jamaica. If it is indeed from Hispaniola, then it seems likely that the type of *P. domingense* will be assignable not to the group of Jamaican plants described above, but rather to the second entity, made up of a group of rather odd plants from Hispaniola. These have uniformly short (often much less than 2 cm) internodes, small leaves, and mostly type 1a inflorescences, with staminate and pistillate flowers intermixed within an internode. The Hispaniolan plants appear to be much stouter and more rigidly upright than the rest of the group. If future workers conclude that the Jamaican plants are a distinct taxon, then the Hispaniolan plants may be distinct as well. However, on the basis of the characters used here, we find full intergradation with the other members of *P. trinervium.*

A third group of plants occurs throughout the Bahamas and the Lesser Antilles. These plants have inflorescences that are predominantly type 1a, with staminate and pistillate flowers intermixed in the same internode. The fruits are orange to red and are generally smooth. This group includes the type of *Phoradendron trinervium* (collected on Martinique), on which the fruits are red. Unlike many of the other members of this entity, the type specimen has minute warts below the sepals.

A fourth group of plants is predominantly Lesser Antillean and has leaves that are broadly ovate or even suborbicular. Sterile specimens often cannot be reliably distinguished from small-leaved specimens of *Phoradendron anceps. Phoradendron trinervium* rarely has the type 1d or 1e inflorescence common in *P. anceps,* and the stem is rhombic and soon terete (vs. clearly compressed in *P. anceps*). In more mature plants the distinction becomes clear, because the fruits of *P. anceps* soon develop their characteristic golden sheen and pyriform shape; the sepals remain closed or only slightly open, but not stiffly erect as in *P. trinervium.* The mature fruits of *P. anceps* are white to cream colored, whereas those of *P. trinervium* are yellow, orange, or red-orange.

A fifth group of plants occurs on Jamaica; it has leaves that are widest at the middle and tapering to both ends, rather than obovate or oblanceolate. These plants often have only one pistillate flower per bract and include the isotypes (but not the holotype) of *Phoradendron campbellii.*

24. **Phoradendron undulatum** (Pohl) Eichler *in* C. Martius, Fl. Brasil. **5**(2): 122. *t. 39.* 1868. FIGURE 4f.

Viscum undulatum Pohl *in* DC. Prodr. Syst. Nat. Regni Veg. **4:** 282. 1830. TYPE: Brazil, 1828, *Pohl 868* (holotype, G-DC, IDC 800. 664: I. 5!).

Phoradendron herminieri Trel. Genus *Phoradendron,* 131. 1916. TYPE: Guadeloupe, *Duss 3904, pro parte* (holotype, US, photo at ILL!); specimen at NY is designated *P. chrysocarpum* var. *dussii* but is *P. anceps.*

Phoradendron chrysocarpum Krug & Urban var. *stehlei* Trel. *in* Stehlé, Bull. Soc. Bot. France **92:** 262. 1945. TYPE: Guadeloupe, *H. & M. Stehlé 2459* (holotype, ILL!; isotypes, GH!, NY!, P!).

Stems flattened; cataphylls generally 2 pairs on lateral branches only (these sometimes confused with main axes because 1 of pair often aborts), first pair 2–3 mm above node, second ca. 25 mm above first, shallowly 3-lobed, spreading. Leaves with petiole 4–5 mm long; blade lanceolate, 6–12.5 × 2.2–4.3 cm, thin, apex acuminate, base cuneate, nerves pinnate. Inflorescences 1 to 3 per leaf axil, to 5 cm long, axis < 1 mm thick when dry; cataphylls 1 to 5 pairs, boat shaped to crateriform like bracts; fertile internodes up to 9, type 1a; flowers 5 to 7 per bract, staminate and pistillate intermixed; apical flower 2/1, lower ones 1/2. Fruits globose, white, becoming rough-wrinkled when dry; sepals somewhat parted.

DISTRIBUTION. Costa Rica, Panama, Venezuela, Peru, Brazil, Bolivia, Guadeloupe, Dominica, Martinique.

We have found no way to distinguish the Caribbean from the South American members of this taxon and therefore place Trelease's name, *Phoradendron herminieri,* in synonymy; Kuijt (1964) reached a similar conclusion. Trelease erected the species on the basis of its glossy leaves on dried specimens, a character we have not found distinctive.

25. **Phoradendron wattii** Krug & Urban *in* Urban, Bot. Jahrb. Syst. **24:** 43. 1897. TYPE: Jamaica, 14 December 1890, *A. Hitchcock s.n.* (lectotype (Trelease, 1916), B, destroyed; isolectotype, MO, photo at ILL!).

FIGURE 4g, h.

Phoradendron wattii Krug & Urban var. *producta* Trel. Genus *Phoradendron,* 100. 1916. TYPE: Jamaica, Portland Point and Rocky Point, 5 March 1908, *Harris 10188* (holotype, B, destroyed, photo at ILL!; isotypes, K!, NY!, P!).

Phoradendron campbellii Krug & Urban *in* Urban, Bot. Jahrb. Syst. **24:** 44. 1897. TYPE: Jamaica, Wareka Road, 10 August 1896, *Campbell 6398* (holotype, B, destroyed, photo at ILL!). Isotypes at BM! and NY! are *P. trinervium.* Note by Trelease on NY specimen: "This, however, is really *P. domingense*; and probably part of no. 6383 of same place and date."

Viscum flavens Macfad. Fl. Jamaica **2:** 195. 1850; not Sw. 1788, or Sprengel, [1824] 1825. TYPE: Jamaica, *Macfadyen s.n.* (holotype, K!).

Phoradendron berterianum sensu A. Hitchc. Annual Rep. Missouri Bot. Gard. **4:** 125. 1893, *fide* Urban (1897).

Stems flattened; internodes frequently only 10–15 mm on lateral branches; cataphylls 1 to 3 pairs, on lateral branches only, 2–4 mm distal to node, broadly deltate to ovate, flaring, lobed to bifid. Leaves with petiole 5–10 mm long; blade lanceolate to elliptic, oblong, or oblanceolate, 3–8 × 1.1–3 cm, the apex rounded and truncate to tapering and somewhat acute or acuminate, occasionally apiculate, the base tapering, the nerves basal. Plants dioecious; inflorescences 1 to 3 per leaf axil, to 2 cm long in pistillate plants, axis 2–3 mm

thick when dry, 3.5 cm long in *Harris 10188* (a staminate plant); cataphylls lacking or 1 pair, spreading like bracts; fertile internodes 2 to 4 (or 5); pistillate inflorescence with 1 flower in 1-mm-deep cup above each bract (sometimes in triads); staminate inflorescence type 1a, with 5 to 11 flowers per bract; orientation 2/1 if flowers solitary, apical flower 2/1 and lower ones 1/2 if in triads or type 1a arrangement. Young fruits pyriform, drying blue-glaucous with lighter-colored sepals; mature fruits pale yellow; sepals closed, parting slightly at maturity.

DISTRIBUTION. Endemic to Jamaica.

As described here, this species is unusually variable in leaf shape but can easily be recognized by the distinctive fruits.

NOMINA EXCLUDENDA

Loranthus sessilis Sprengel, MS in hb. Balbis, *nomen nudum.* Cited in Trelease (1916).

Loranthus torulosus Kunth *in* Humb., Bonpl., & Kunth, Nova Gen. Sp. Pl. **3:** 443. 1818. TYPE: Colombia, Popayán, *Bonpland 3808* (P-HBK!, IDC 6209-2. 88: III. 7). This has been placed by some authors in the synonymy of *Phoradendron piperoides.* It is excluded because the type has a type 1b inflorescence on some internodes and the leaves are rounded.

Loranthus viscifolius Kunth *in* Humb., Bonpl., & Kunth, *ibid. Phoradendron viscifolium* (Kunth) Trel. Genus *Phoradendron,* 109. 1916. "Crescit cum praecedente." TYPE: [Ecuador, Guayaquil,] *Bonpland 3798* (P-HBK!, IDC 6209-2. 89: I. 1). Although this name was placed in the synonymy of *P. quadrangulare* by Krug and Urban (*in* Urban, 1897), we believe it to be distinct because of the strongly oblanceolate leaves.

Phoradendron antillarum Trel. var. *latum* Trel. Repert. Spec. Nov. Regni Veg. **26:** 343. 1929, *nomen nudum.* In synonymy of *P. cauliflorum.*

Phoradendron buxifolium (Lam.) Griseb. Mem. Amer. Acad. Arts **8:** 191. 1861. = **Dendrophthora buxifolia** (Lam.) Eichler. Although Grisebach transferred *Viscum buxifolium* Lam. to *Phoradendron,* Kuijt (1961) followed Eichler in correctly placing this species in *Dendrophthora.* He also neotypified Lamarck's name with *C. Wright 220a* (GH!).

Phoradendron buxifolium (Lam.) Griseb. var. *rotundata* C. Wright ex Griseb. Catal. Pl. Cubens. 120. 1866. TYPE: Cuba, *C. Wright 2649* (holotype, GH!). = **Dendrophthora buxifolia** (Lam.) Eichler.

Phoradendron cayennense Eichler *in* C. Martius, Fl. Brasil. **5**(2): 129, 134m. 1868. TYPE: "e silvis Cayennae," hb. L. C. Rich. Trelease (1916) assigned this species to the synonymy of *P. racemosum.* There are several specimens labeled *P. cayennense* in hb. Rich. at P, but none is referable to *P. racemosum.*

Phoradendron constrictum Griseb. Mem. Amer. Acad. Arts **8:** 192. 1861. TYPE: in Cuba Orientali, prope Monte Verde, *C. Wright 220b* (holotype, K!; isotype, GH!). = **Dendrophthora constricta** (Griseb.) Eichler.

Phoradendron crassifolium (Pohl) Eichler *in* C. Martius, Fl. Brasil. **5**(2): 125.

1868. This was figured by Eichler as having inflorescences with triads at the top and the bottom, and a type 1b arrangement at the middle internodes. Eichler described the spikes as being "2 × (7–5-) floris, floribus 2×2 vel 2×3 seriatis." This inflorescence arrangement is different from that of *P. martinicense.* Eichler also drew the berries as smooth; those of *P. martinicense* are rough-warty. See also discussion under *P. martinicense.*

Phoradendron giordanae Warb. Tropenpflanzer **9:** 635. 1905, *nomen nudum.* Cited by Trelease (1916) in the synonymy of *P. dichotomum* and "lectotypified" by him with a Venezuelan plant, *Knoop iii, a* (B, destroyed, photo at ILL!). The lectotype appears to have an abnormally enlarged globose inflorescence. Either the plant is galled, or the inflorescence morphology is very different from that of *P. dichotomum.*

Phoradendron hexastichum (DC.) Griseb. var. *latifolium* Griseb. Catal. Pl. Cubens. 120. 1866. Cited in Trelease (1916) as a synonym of *P. racemosum,* apparently an error. Grisebach described no varieties under *P. hexastichum,* although on the same page he listed *P. latifolium,* which is referable to *P. piperoides* (Kunth) Trel.

Phoradendron juniperinum Engelm. Mem. Amer. Acad. Arts, n.s. **4:** 58. 1849. TYPE: New Mexico, Santa Fe, 1847, *Fendler 281* (holotype, MO, not seen). In the first edition of the *Index Kewensis,* this species is listed as occurring in the West Indies, but this is obviously in error. We have seen no specimens or any other reports of its occurrence there.

Phoradendron lamprophyllum Urban, Repert. Spec. Nov. Regni Veg. **21:** 54. 1925. TYPE: Cuba, Prov. Oriente, sierra de Cristal, 1100–1325 m, *Ekman 15983* (S, not seen). = **Dendrophthora hians** Urban, *fide* Kuijt (1961).

Phoradendron macrostachyum (Jacq.) Griseb. Fl. Brit. W. Indian Is. 314. 1860. Type of *Viscum macrostachyon* Jacq. is Collectanea, *t. 5, fig. 3.* 1789. Kuijt (1961) incorrectly reported the transfer of the epithet to *Phoradendron* as "*P. macrostachyum* (Sprengel) Griseb., Cat. Pl. Cub. 120, 1866." Sprengel ([1824] 1825) attributed *V. macrostachyon* to Jacquin (1789), who first published the epithet and cited a plant from Martinique. Grisebach then transferred the name to *Phoradendron* in 1860 (cited above), and Eichler transferred Jacquin's name to *Dendrophthora* in 1868. The type should be Jacquin's plate. Although Kuijt (1961) placed these names in the synonymy of *Dendrophthora flagelliformis* (Lam.) Krug & Urban, that species does not occur on Martinique. Jacquin's plate depicts a plant fitting the description of *D. martinicensis* Kuijt. The Jacquin name thus takes priority, and *D. martinicensis* should be relegated to the synonymy of *D. macrostachya* (Jacq.) Eichler.

Phoradendron macrostachyum (Jacq.) Griseb. f. *parvifolia* Griseb. Catal. Pl. Cubens. 120. 1866. TYPE: *C. Wright 2652* (holotype, GOET!; isotype, GH!). = **Dendrophthora serpyllifolia** (Griseb.) Krug & Urban.

Phoradendron pepericarpum A. Gray, U. S. Expl. Exped., Phan. 742. 1854. TYPE: Brazil, *Wilkes Exped. s.n.* (GH!). This species has been cited as being synonymous with both *P. crassifolium* (Pohl) Eichler and *P. mar-*

tinicense (DC.) Griseb., but it has a type 1b inflorescence. It may be synonymous with the former, but it is not with the latter.

Phoradendron rehderianum Urban, Ark. Bot. **23A**(5): 62. 1930. TYPE: Cuba, Gavilán, prov. Santa Clara, 12 March 1928, *Rehder 1209* (holotype, B, destroyed; isotype, NY!). Kuijt (1961) determined this as a species of *Dendrophthora.*

Phoradendron serpyllifolium Griseb. Mem. Amer. Acad. Arts **8:** 192. 1861. TYPE: Cuba, near Monte Verde, *C. Wright 1254* (holotype, GOET!; isotype, GH!). = **Dendrophthora serpyllifolia** (Griseb.) Krug & Urban.

Phoradendron serpyllifolium Griseb. var. *aphyllum* Griseb. *ibid., nomen nudum* (*C. Wright 224* cited in original publication). = **Dendrophthora cupressoides** (Macf.) Eichler.

Phoradendron sessilifolium Griseb. *ibid.* 191. TYPE: Cuba, near La Perla, *C. Wright 1301* (holotype, GOET!; isotype, GH!). = **Dendrophthora sessilifolia** (Griseb.) Krug & Urban.

Phoradendron testifolium C. Wright ex Griseb. Catal. Pl. Cubens. 120. 1866. TYPE: in Cuba Orientali, prope Monte Verde, *C. Wright 2648* (holotype, GOET!; isotype, GH!). = **Dendrophthora constricta** (C. Wright ex Griseb.) Eichler.

Phoradendron tetrastachyum Griseb. Mem. Amer. Acad. Arts **8:** 191. 1861. TYPE: in Cuba Orientali, prope Monte Verde, *C. Wright 218, pro parte* (holotype, GOET, not found; isotype, GH!). = **Dendrophthora tetrastachya** (Griseb.) Urban.

Phoradendron zuloagae Trel. Genus *Phoradendron,* 105. 1916. TYPE: Venezuela, Caracas, 1915, *Zuloaga s.n.* (photo! in Trelease, 1916, *pl. 150a*). No herbarium cited, not at ILL. This has been placed by some authors in the synonymy of *P. quadrangulare* (Kunth) Krug & Urban; we exclude it because of its erect sepals.

Viscum ellipticum Presl, Epimel. Bot. 254. 1849, *nomen nudum.* Cited by Trelease (1916), with an unnumbered Haenke specimen from Mexico as "type" (PR, photo at ILL!). This is an error because Presl never published a species by this name.

Viscum kunthianum DC. Prodr. Syst. Nat. Regni Veg. **4:** 283. 1830. TYPE: "in arboribus prope Guayaquil Quitensium." No specimen in G-DC. Based on *V. trinervium* Sprengel, *pro parte,* and *Loranthus viscifolius* Kunth, both placed in the synonymy of *Phoradendron quadrangulare* by Krug and Urban (*in* Urban, 1897). We have excluded *L. viscifolius* from *P. quadrangulare* because of leaf shape, and we thus exclude *V. kunthianum* pending designation of a type.

Viscum latifolium Lam. Encycl. Méth. Bot. **3:** 57. 1789; not Sw. 1797, or others. TYPE: P-LAM, IDC 6207-15. 578: I. 7!. Not found at P. = **Phthirusa** sp. Has been cited as a synonym for *Phoradendron racemosum.*

Viscum salicifolium Presl, Epimel. Bot. 254. 1849. *Phoradendron salicifolium* (Presl) Eichler *in* C. Martius, Fl. Brasil. **5**(2): 110. 1868. TYPE: Quito, *Haenke* (holotype, PR, photo!). Placed in the synonymy of *P. quadrangulare* by Trelease (1916). The protolog is not diagnostic, and the pho-

tograph of the type does not show enough detail for certain identification; however, the leaves appear to be the wrong shape for *P. quadrangulare.*

Viscum saururoides DC. Prodr. Syst. Nat. Regni Veg. **4:** 280. 1830. *Phoradendron latifolium* (Sw.) Griseb. var. *saururoides* (DC.) Griseb. Fl. Brit. W. Indian Is. 314. 1860, *nomen confusum.* TYPE: in Cayenne, *Patris s.n.* De Candolle based his species in part on *V. latifolium* Lam., for which the type is a specimen of *Phthirusa,* and in part on "*V. racemosum* Aubl.?" The specimens of *V. saururoides* in G-DC (IDC 800. 663: II. 2, 3) can be referred to *Phoradendron piperoides.* Urban (1897) placed this name in the synonymy of *P. racemosum,* based on De Candolle's citation of Aublet.

Viscum trinervium Sprengel, Syst. Veg. ed. 16 [17]. **1:** 488. [1824] 1825, not Lam. Type not found. This species was associated with *Loranthus viscifolius* in the synonymy of *V. kunthianum* DC.

Philcox (1978) also listed *Phoradendron ayliffii* (as *ayliffi*) Philcox, *P. fanshawei* Maguire, *P. obtusissimum* (Miq.) Eichler, and *P. perrottetii* (DC.) Eichler as occurring on Trinidad. We found no Trinidad specimens of these at K and have been unable to obtain the specimens at TRIN cited by Philcox. Since the first is endemic to Trinidad and the latter three are predominantly South American, they would be better treated in a monograph including the South American phoradendrons.

UNPLACED SPECIMENS

Grand Cayman: alt. 10–20′, Aug. 1938, *Kings GC-388* (NY). In some respects similar to *Phoradendron rubrum,* but sepals closed and leaf apices acute; also close to *P. quadrangulare,* but leaves unusually broad for their length.

Hispaniola: wet woods near Ciénaga de la Culata, Constanza, alt. 1500–1600 m, parasitic on *Symplocos berterii,* 29 Nov. 1969, *Liogier 17139* (GH, NY). Sterile; venation not apparent; cataphylls small, unusually far above the node.

Trinidad: heights of St. Anne, 11 April 1920, *Britton & Hazen 1691* (GH). Sterile; leaf shape variable; not obviously assignable to any species.

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APPENDIX. **Index to specimens seen.**

(1) *Phoradendron anceps*; (2) *P. barahonae*; (3) *P. carneum*; (4) *P. dichotomum*; (5) *P. flavens*; (6) *P. gracile*; (7) *P. grisebachianum*; (8) *P. gundlachii*; (9) *P. haitense*; (10) *P. hartii*; (11) *P. hexastichum*; (12) *P. inequidentatum*; (13) *P. martinicense*; (14) *P. mucronatum*; (15) *P. northropiae*; (16) *P. ottonis*; (17) *P. piperoides*; (18) *P. quadrangulare*; (19) *P. racemosum*; (20) *P. rubrum*; (21) *P. solandrae*; (22) *P. tetrapterum*; (23) *P. trinervium*; (24) *P. undulatum*; (25) *P. wattii.*

Abbott 400 (1), *950* (18), *2777* (19).
Alexander s.n. at K (7).
Allard 15757 (18).
Anderson & Sternberg 3077 (17), *3429* (5).
Arnoldo 1023 (23).
Augusto 418 (17), *623* (18), *761* (18), *822* (18), *1253* (4), *1418* (18).
Ayliffe 14320 (12), *14371* (17), *14699* (16), *16499* (19).
Baker 2559 (18), *2602* (17), *14595* (19), *14606* (13).
Ball s.n. in 1882 (6).
Barclay & Proctor 38471 (23).
Barkley 3870 (25).
Baudin s.n. at P (23).
Beard 620 (23), *1103* (23), *1132* (13), *1420* (23).
Belanger 267 (23).
Bena 555 (23), *556* (23), *s.n.* in 1944–1946 (5, 23).
Bertero 439 (1), *710* (4), *1234* (18), *s.n.* in 1820 (19, 23), *s.n.* in 1821 at G-DC (14), *s.n.* at G-DC (14).
Biolley 7078 (17).
Boldingh 1660B (23).
Bonpland s.n. at P-HBK (17), *s.n.* at P-HBK (18).
Brace 3428 (20), *4461* (20), *4643* (20), *5325* (15).
Britton 180 (5), *355* (25), *807* (23), *813* (22), *965* (7), *977* (7), *1889* (19), *1895* (23), *1927* (23), *1950* (18), *1985* (18), *2052* (18), *2119* (18), *2415* (18), *2687* (17), *2718* (14), *2719* (1), *2840* (18), *2991* (18), *3068* (23), *3144* (7), *3215* (7), *3283* (18), *3383* (7), *3668* (18), *3703* (25), *3734* (25), *3765* (25), *3773* (23), *3795* (23), *3905* (23), *3968* (5).
Britton & Brace 832 (20).
Britton & Britton 7352 (1), *7425* (19), *7837* (17), *7904* (17), *8058* (1), *8799* (19), *9561* (1), *10049* (18).
Britton, Britton, & Boynton 8292 (1).
Britton, Britton, & Brown 5817 (18), *5850* (1), *5854* (23), *6012* (2), *6235* (1), *6423* (23).
Britton, Britton, & Cowell 10241 (18), *13106* (8).
Britton, Britton, & Hazen 1001 (13).
Britton, Britton, & Marble 1946 (1).
Britton, Britton, & Wilson 4687 (18), *5579* (18).
Britton & Bruner 7547 (11).
Britton & Cowell 1293 (23), *1301* (1), *1352* (1), *1940* (18), *4127* (11), *4131* (4), *12553* (18).

Britton, Cowell, & Brown 3918 (19), *4348* (18), *4570* (1), *4578* (18), *4814* (23), *4816* (1).
Britton, Cowell, & Shafer 12919 (18), *12928* (17).
Britton, Earle, & Wilson 4585 (18).
Britton, Freeman, & Brown 2760 (23).
Britton, Freeman, & Watts 2701 (16), *2708* (16).
Britton & Hazen 1691 (23), *1726* (16).
Britton, Hazen, & Mendelson 1288 (5), *1800* (5).
Britton & Hollick 1861 (7), *1890* (23), *2772* (7).
Britton & Marble 2245 (18), *2248* (23).
Britton, Matz, & Chardon 6873 (11).
Britton & Millspaugh 5867 (20), *6325* (20).
Britton & Shafer 1640 (1), *1644* (18), *1831* (1), *1844* (23).
Britton, Stevens, & Hess 2470 (17), *2535* (19), *2564* (22), *2569* (11).
Britton & Wilson 4886 (18), *5147* (4), *5327* (4), *5644* (18).
Britton, Wilson, & Léon 15313 (18).
Broadway 1843 (17), *1864* (11), *1873* (17), *2265* (18), *2596* (13), *3982* (17), *4528* (17), *6013* (17), *6145* (1), *6626* (13), *6945* (18), *7396* (5), *7468* (5), *7546* (17), *7574* (16), *7617* (23), *7708* (13), *7709* (23), *7914* (1), *8084* (23), *8976* (10), *9088* (1), *9148* (18), *9692* (18), *9693* (17), *s.n.* in 1895 (11), *s.n.* in 1918 (17), *s.n.* on 19 Sept. 1918 (18).
Broeder 1972 (23).
Brown 51 (7), *394* (18).
Campbell 6398 (B, 25; BM, NY, 23), *6604* (1), *6605* (23).
Claussen 252 (14).
Clemente 2705 (6), *3443* (18), *4327* (18), *4406* (17), *6082* (18), *6417* (17), *6445* (18), *7178* (18).
Clemente & Liogier 4075 (17).
Coker 303 (20), *558* (20).
Combs 299 (18), *347* (20), *348* (20).
Cooley 8217 (23), *8718* (17).
Correll 41617 (23), *41719* (23), *43463* (20), *43845* (23), *44495* (20), *45843* (23), *45851* (23), *46047* (23), *46410* (23), *47412* (23), *47418* (23), *48366* (20), *48382* (23), *49396* (15), *49954* (23), *49975* (23).
Correll & Correll 48129 (20), *50546* (20), *51033* (18).
Correll & Evans 43978 (20).
Correll & Popenoe 42708 (20), *51421* (20).
Correll & Proctor 47802 (20), *47812* (15), *47876* (20), *48709* (20), *48890* (20).
Correll & Sauleda 50452 (23).
Cowan 1403 (17), *1449* (23), *1536* (17), *1594* (23).
Cowan & Forster 1466 (17).
Cowell 626 (19), *753* (18).
Crawford 783 (7).
Crosby, Hespenheide, & Anderson 249 (25), *466* (7).
Crueger 111 (5), *s.n.* at K (18).
Curran & Haman 87 (23).
Day 320 (18), *331* (17).
Dunbar 60 (23), *298* (23).
Duss 100 (14), *101* (A, 24; GH, 1), *1372* (14), *1373* (23), *1374b* (NY, 1; NY, 13), *1375* (11), *2966* (NY, 13; NY, 24), *2968* (GH, 23; NY, 1), *2969* (NY, 1; NY, 13), *2969b* (1), *3852* (14), *3891* (13), *3902* (NY, 1; NY, 13), *3904* (24), *4099* (23), *4137* (11), *4137a* (13), *4156* (14), *4157* (GH, 13; NY, 24), *4415* (11), *4417* (NY, 1; NY, 23), *4418* (GH, 24; NY, 1).
Eggers 93 (23), *661* (5), *880* (1), *926* (1), *946* (5), *1184* (18), *1651* (18), *1682* (2), *1741* (19), *1845* (4), *1895* (2), *2011* (19), *3847* (20), *4668* (17), *4778* (18), *4840* (17), *4902*

(17), *6140* (11), *6396* (17), *6398* (14), *6746* (5), *s.n.* in Feb. 1883 (3), *s.n.* in Dec. 1883 (3).
Egler 39-169 (14).
Ehrenberg s.n. at NY (18).
Ekman 340 (9), *413* (1), *706* (18), *1495* (18), *1523* (18), *1954* (17), *2186* (18), *2828* (19), *4136* (17), *4460* (1), *5076* (11), *5150* (11), *5750* (11), *6243* (18), *6443* (14), *6492* (1), *6666* (17), *6708* (14), *7217* (19), *9083* (22), *9180* (18), *9370* (17), *9589* (14), *9601* (1), *9604* (9), *9615* (1), *9626* (18), *9978* (20), *10482* (17), *10695* (4), *10696* (17), *11342* (4), *11402* (18), *12343* (18), *13710* (18), *14306* (17), *14462* (8), *14721* (20), *14795* (17), *14919* (17), *16276* (11), *18382* (18), *19134* (1).
Ernst 1107 (17), *1180* (23), *1202* (13), *1365* (23), *1572* (23), *1583* (13), *1640* (14).
Eyerdam 317 (14), *363* (5), *506* (4).
Faris 158 (18).
Fendler 651 (18), *654* (17), *1810* (18).
Fishlock 52 (23).
Focke s.n., photo at K (19).
Forsstrom s.n. at NY (23).
Fuertes 240 (14), *275* (A, NY, P, 2; BM, K, 19), *383* (18), *827* (18), *927* (2), *1393* (14), *1531b* (2).
Gallo 522 (23).
Garber 11 (2), *24* (18).
Gillis 8980 (17), *8992* (7), *11683* (23), *12076* (23), *12990* (20).
Gillis & Proctor 11548 (20).
Guilding s.n. in 1826 at GH (23), *s.n.* at K (5), *s.n.* at K (11), *s.n.* at K (23).
Haenke s.n. at PR (11).
Hahn 296 (BM, K, P, 14; GH, K, P, 23), *298* (13), *550* (1), *733* (1), *1092* (23), *1385* (14), *1386* (11), *1870* (23).
Haney 1824 (23).
Hansen s.n. at NY (18).
Harris 6203 (5), *6341* (7), *6376* (7), *6383* (23), *6392* (6), *6393* (22), *6395* (25), *6599* (25), *6659* (1), *6676* (23), *6680* (25), *6703* (1), *6781* (23), *6926* (22), *7264* (23), *8138* (23), *9220* (7), *9568* (23), *9696* (25), *10175* (23), *10188* (25), *10202* (7), *10339* (17), *10861* (7), *s.n.* at NY (25).
Harris & Britton 10519 (25), *10529* (23).
Harris & Lawrence C155283 (5).
Hart s.n. in 1896 at P (10), *6113* (17), *6117* (10).
Heller 6161 (23), *6186* (18), *6188* (1).
Heller & Heller 205 (18), *514* (19).
Hess 675 (11).
Hill 121 (17), *3172* (15), *3181* (20).
Hioram 1306 (18), *1832* (18), *1910* (17), *2021* (17), *2080* (18), *2112* (17), *4093* (11), *7593* (1), *7596* (17), *s.n.* at NY (1), *s.n.* at NY (18).
Hioram & Maurel 2418 (17), *2508* (17).
Hitchcock s.n. in 1890 at B (destroyed; photo at ILL) (25).
Hodge 650 (23), *1149* (1), *1439* (13), *3981* (5).
Hodge & Hodge 1832 (5), *2085* (13), *2231* (14), *2233* (14), *2524* (23), *2975* (5), *3784* (23).
Holdridge 1002 (9), *1842* (11).
Howard 4805 (18), *4806* (18), *6627* (18), *10760* (23), *10853* (23), *11023* (23), *11191* (5), *11349* (23), *11510* (1), *11670* (5), *12091* (18), *18243* (23), *18375* (23).
Howard & Howard 8213 (14), *8732* (4), *8782* (19), *8837* (2), *9504* (18), *9676* (18), *18037* (17), *18798* (11), *18853* (23), *18871* (11), *18888* (17), *19384* (13), *19427* (5), *19530* (17).
Howard, Howard, & Howard 18933 (23), *19041* (23).

Howard & Nevling 15950 (1), *16013* (11).
Howard & Proctor 13541 (17), *14244* (17).
Howard, Proctor, & Stearn 14744 (23), *14916* (7).
Hunnewell 18824 (17).
Hunnewell & Griscom 14301 (17).
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Jenman 4678 (12).
Jérémie 1131 (5), *1158* (23), *1206* (23).
Jiménez 1745 (18), *5163* (18), *8110* (18).
Johnston 127 (23), *999* (23), *2029* (19), *2057* (22).
Judd 614 (7).
Kimber 917 (23).
Kings 14 (18), *365* (18), *CB91* (18), *CB91A* (18), *LC36* (20), *LC43* (20).
Kostermans A15042 (13).
Kuntze 210 (19), *363* (4), *415* (19), *426* (22), *495* (18).
Laudat s.n. at K (24).
Lavastre 1904 (14), *1909* (18).
Leibold s.n. at PR (17).
Léon 162 (17), *352* (18), *3738* (18), *7249* (18), *7842* (18), *8128* (18), *11075* (8), *22820* (20), *72380* (18).
Léon & Cazanas 5909 (18).
Léon & Roca 7249 (18), *7400* (22), *7842* (18), *7849* (17), *8128* (18).
Léon & Victorin 20508 (17).
Léon, Victorin, Clemente, & Liogier 20015 (17).
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Leonard & Leonard 12198 (K, 19; NY, 11), *12574* (18), *12670* (18), *13144* (18), *13661* (1), *14710* (14), *14760* (14).
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Liogier 1085 (17), *1631* (23), *4077* (18), *9122* (23), *9137* (23), *9215* (17), *9305* (1), *9729* (18), *9876* (17), *10000* (11), *10563* (1), *10593* (1), *10634* (1), *10635* (22), *10763* (11), *11045* (4), *11112* (18), *11256* (4), *11305* (11), *11682* (14), *12351* (18), *12361* (4), *12490* (17), *12531* (18), *12649* (14), *12730* (2), *12969* (4), *13204* (19), *13393* (22), *13553* (4), *13593* (18), *13911* (18), *13939* (4), *13969* (4), *14037* (14), *14141* (14), *14317* (4), *14962* (14), *15208* (14), *15570* (14), *15837* (11), *16294* (2), *17043* (1), *17582* (2), *17583* (4), *17585* (18), *17880* (14), *18459* (11), *18541* (17), *19842* (18), *20810* (18), *20831* (4), *21318* (18), *21685* (11), *22515* (2), *26742* (23), *26877* (4).
Liogier & Clemente 978 (17).
Liogier & Liogier 1940 (17), *18737* (19), *18895* (18), *19397* (4), *20493* (23), *20514* (14), *21612* (14), *22518* (14), *22521* (19), *23477* (4), *23945* (4), *24492* (19), *24892* (18), *25170* (1), *25401* (23), *25486* (4), *26742* (23), *29500* (17), *29929* (17), *30895* (11), *30936* (17), *30941* (11).
Liogier, Liogier, & Jiménez 8244 (23).
Liogier, Liogier, & Martorell 28178 (19), *28362* (1).
Liogier, Liogier, & Solano 30776 (2), *30780* (18), *30795* (2).
Liogier, Vivaldi, & Diaz 27924 (23).
Lloyd 207 (24), *208* (5), *463* (23), *764* (14), *765* (11), *913* (23).
Luna 163 (2), *358* (11), *596* (8), *692* (11), *8059* (2).
Lunt 6616 (18).
Macfadyen s.n. at K (5), *s.n.* at K (23), *s.n.* at K (25).
Marble 231 (25).

Marcano & Jiménez 5451 (11).
March 938 (18), *942* (17), *1316* (23).
Maxon 1675 (18), *4337* (17).
Maxon & Killip 681 (5), *1055* (25).
McDale s.n. at BM (20).
Morton 5682 (23), *5729* (23).
Mouret 275 (23).
Nash 98 (14), *150* (19), *633* (4).
Nash & Taylor 947 (23), *1021* (23), *1151* (4), *1251* (17), *1314* (23), *1322* (18), *1342* (23), *1529* (14), *1580* (14).
Nicholson s.n. (23).
Norman 191 (18), *247* (5).
Northrop & Northrop 551 (15), *740* (19).
Orcutt 3867 (25).
De la Ossa s.n. in 1825 at G-DC (11), *s.n.* at G-DC (17).
Perrottet s.n. in 1824 at G-DC (23).
Philcox 7549 (17).
Philcox & Kalloo 7171 (22), *7172* (18), *7180* (13), *7211* (5), *7321* (17).
Philcox, Kalloo, & Jurawan 7387 (13).
Philcox & Wood 7069 (17).
Philcox, Wood, & Kalloo 7517 (10).
Phillipson 696 (7), *792* (5).
Picarda 1666 (9).
Plée 218 (18), *501* (17), *576* (18), *s.n.* at P (19), *s.n.* at P (1), *s.n.* at P (23).
Poeppig s.n. at K (18), *s.n.* at P (18).
Pohl 868 (24), *4319* (17).
Prax s.n. in 1859 at P (18).
Preneloup 507 (19), *570* (18).
Pringle 80 (18), *1854* (3).
Prior 607 (6).
Proctor 6116 (7), *6503* (23), *9172* (23), *9484* (23), *9521* (5), *10179* (25), *10253* (25), *11628* (7), *11696* (1), *15111* (23), *15259* (20), *15680* (22), *16099* (23), *16703* (7), *17037* (5), *17589* (13), *17876* (23), *17983* (11), *18016* (23), *18089* (2), *18564* (1), *19043* (23), *20319* (24), *20731* (23), *21252* (23), *24783* (25), *26042* (11), *27521* (6), *27540* (23), *27608* (25), *27615* (25), *27631* (25), *28020* (23), *28959* (20), *31710* (17), *33544* (6), *33545* (1), *33646* (4), *33812* (7), *34197* (23), *34967* (1), *35075* (23), *35100* (23), *35194* (18), *35463* (25), *36352* (4), *36454* (1), *36898* (20), *37276* (25), *37430* (21), *37474* (21), *37592* (21), *37603* (21).
Proctor & Gillis 33352 (23), *33917* (23).
Proctor & Mullings 21983 (7).
Questel 223 (23), *2293* (13), *4102* (1), *4193* (23).
Ramage s.n. at BM (17), *s.n.* at K (24).
Raynal-Roques & Jérémie 21294 (1).
Rehder 1214 (18), *s.n.* on 13 Feb. 1903 (A, 6; A, GH, 25).
Ricksecker 302 (1), *304* (19), *s.n.* at GH (1).
Roig 3889 (18).
Roig & Cremata 2198 (11).
Rose, Fitch, & Russell 3353 (23), *3701* (18), *3852* (23), *3993* (14).
Rugel 165 (18), *269b* (18), *270* (17).
Rusby 1544 (12).
Sagra s.n. at P (18).
Sandwith 1741 (17), *1809* (23).
Sastre 5394 (23), *6520* (11).
Sastre & Fournet 2519 (23), *2656* (A, 24; P, 1).

Sastre & Sastre 4309 (5).
Shafer 159 (18), *296* (20), *314* (23), *320* (23), *331* (17), *363* (18), *371* (20), *563* (18), *600* (23), *607* (23), *815* (18), *1109* (18), *1622* (18), *2003* (23), *3270* (17), *3427* (17), *8116* (17), *8517* (17), *8582* (17), *8590* (11), *8601* (17), *8737* (17), *8817* (4), *11823* (18), *11828* (18), *12109* (18), *12178* (8), *12403* (18).
Shafer & Fitch 1472 (1).
Sieber 227 (BM, K, P, 11; G-DC, 13).
Sintenis 339 (17), *339b* (1), *885* (18), *887* (23), *1270* (17), *2347* (19), *2348* (4), *2836* (11), *3035* (18), *3058* (4), *3246* (23), *3428* (23), *4154* (17), *4288* (4), *4614* (17), *5383* (11), *5562* (18), *5926* (19), *6060* (1), *6114* (4), *6758* (22), *s.n.* in Jan. 1885 (18), *s.n.* in Feb. 1885 (1), *s.n.* in Dec. 1885 (4), *s.n.* on 1 Jan. 1886 (23), *s.n.* in Jan. 1886 (19), *s.n.* in Feb. 1886 (4), *s.n.* in April 1886 (22), *s.n.* in Oct. 1886 (2), *s.n.* in Feb. 1888 (4).
Small & Carter 8479 (15).
Smith 10154 (23), *10189* (23), *10315* (14), *10492* (23).
Smith & Smith M34 (23), *245* (17), *248* (17), *297* (11), *374* (5), *1305* (1), *1306* (23), *1623* (22).
Snow s.n. at K (13).
Spruce 2112 (11).
Squire s.n. on 12 June 1938 (14).
Stearn 805 (23).
Stehlé 49 (17), *70* (23), *73* (23), *117* (23), *373* (1), *374* (14), *375* (14), *1016* (13), *1021* (13), *1035* (NY, P, 13; NY, P, 24), *1130* (13), *1637* (17), *2074* (NY, 13; P, 14), *2162* (24), *2458* (17), *2462* (1), *2489* (23), *2560* (24), *2561* (23), *2562* (24), *2899* (14), *2900* (1), *2903* (14), *2904* (14), *2944* (23), *5627* (13), *6249* (23), *6450* (11), *6608* (17), *7228* (11), *s.n.* at A (23).
Stehlé & Stehlé 2452 (1), *2459* (24), *3368* (1), *6585* (11), *77/25* (23).
Stevens & Hess 3107 (1), *3301* (1).
Stevenson 2098 (1).
Stimson 1484 (19), *2033* (17), *3346* (1), *3459* (17).
Stoffers 2555 (23), *3541* (23).
Sturrock 377 (23), *559* (13).
Swartz s.n. at BM (5), *s.n.* at S (5), *s.n.* at S (17).
Taylor 28 (19), *223* (18), *328* (11), *338* (18), *415* (19), *479* (18), *481* (18).
Toepffer 661 (5), *880* (1), *965* (18).
Türckheim 2616 (18), *3284* (11).
Ule 4800 (17).
Underwood & Earle 1311 (17).
Underwood & Griggs 211 (18), *383* (18), *554* (23), *671* (1).
Vaga s.n. at B (destroyed; photo in Trelease, 1916) (14).
Valeur 429 (19), *707* (14), *800* (18).
Van Hermann 4887 (17), *809* (17).
Varanne s.n. in 1851 (14).
Wagner 472 (17), *1372* (1), *1704* (1).
Watt 6219 (5), *6221* (25).
Webster 5598 (5).
Webster & Wilson 4829 (18), *4859* (6).
Weir s.n. on 16 Jan. 1925 (18), *s.n.* on 17 Jan. 1925 (14).
Weir & Faris s.n. on 14 Nov. 1924 (18).
West & Arnold 167 (25), *564* (6), *882* (17), *941* (18).
Wilbur 7713 (10), *7973* (5), *8113* (23), *8280* (23).
Wiles W9 (10), *W30* (10), *W35* (18).
Wilkes Exped. s.n. in 1838–1842 (5).
Wilson 1405 (17), *1748* (18), *7250* (23), *7254* (23), *7315* (23), *7449* (20), *7457* (20), *7532* (20), *7579* (20), *7814* (23), *7851* (23), *s.n.* at K (25).

Winters 562 (18).
Wolcott 2633 (18).
Wood & Atchison 7405 (18).
Woodbury s.n. at NY (17), *s.n.* at NY (18).
Wright 217 (17), *1251* (4), *1251a = 216* (17), *1252* (11), *1300* (K, 20; other *Wright 1300 = Dendrophthora*), *1300b* (20), *1302* (18), *2650* (8), *s.n.* at BM (17).
Wright, Parry, & Brummel 458 (1), *459* (2).
York 253 (5).
Yuncker 17005 (6), *17085* (6).
Zuloaga s.n. at ILL (18).

NOTES RELATING TO THE FLORAS OF NORFOLK AND LORD HOWE ISLANDS, II[1]

P. S. GREEN[2]

After many years when it proved difficult or impossible to devote time to taxonomic research, I have recently been able to return to the study of the floras of Norfolk and Lord Howe islands in the southwestern Pacific.

With a view to writing a Flora of the islands as part of a supplementary volume of the new *Flora of Australia,* I have first undertaken a critical survey and assessment of the indigenous vascular plants, species by species. This has led to a number of taxonomic conclusions and distributional observations, which are set out below under the appropriate families (arranged alphabetically). As the work progresses and, it is hoped, the islands are revisited so that additional field observations can be carried out, yet further notes may be published as precursors to the Flora.

PSILOTALES

Tmesipteris Bernh.

In recent years there has been general agreement that this is not a monotypic genus, although the differences between species are relatively small and great care is needed when distinguishing them. The representatives of the genus on Norfolk Island and on Lord Howe Island are not the same. The Lord Howe Island plant is *Tmesipteris truncata* (R. Br.) Desv., which also occurs in southern Queensland and New South Wales. The Norfolk Island plant, however, needs a new name, because when Endlicher described it in his *Prodromus* and named it *T. forsteri,* he unfortunately included the name *T. tannensis* (Sprengel) Bernh. in its synonymy and thus rendered his name illegitimate by the present Code of Nomenclature. As a replacement I propose the following name.

Tmesipteris norfolkensis P. S. Green, sp. nov.

T. forsteri Endl. Prodr. Fl. Norfolk. 6. 1833, *quoad descr., excl. syn. et typ.*; Spring, Mém. Acad. Roy. Sci. Belgique **24**(Monogr. Fam. Lycopod. 2): 265. 1849; Turner *et al.* Conserv. Norfolk Is. 29. 1962; Leigh *et al.* Rare & Threat. Austral. Pl. 125. 1981. TYPE: Norfolk Island, *Bauer s.n.* (holotype, w!).

Psilotum forsteri (Endl.) Endl. Ic. Gen. Pl. *t. 85.* 1839, *quoad pl. Norfolk., excl. typ.*

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Tmesipteris tannensis sensu Maiden, Proc. Linn. Soc. New South Wales **28:** 740. 1903; *sensu* Laing, Trans. & Proc. New Zealand Inst. **47:** 15. 1915; *non* (Sprengel) Bernh.

ADDITIONAL SPECIMENS EXAMINED. **Norfolk Island:** Red Road toward Mt. Bates, *Green 1377* (A); Mt. Pitt Reserve, between Palm Glen and Red Road, *Lazarides 8086* (K); without further locality, *Cunningham 16* (*62*) (K), *64* (K), *Laing s.n.*, 1917 (CANTY), *Maiden & Boorman s.n.*, 1902 (K), *McComish 46* (K), *Milne 3* (K).

This species can be distinguished from *Tmesipteris tannensis* of New Zealand, with which it has been confused, by its rounded (vs. pointed) synangia; and from *T. elongata* Dangeard, to which it is perhaps most closely related, by its slightly more acute and narrower "leaves" (length-breadth quotients from the specimens at K: 3.8–5, compared with 4.7–6) and by the determinate growth of its fronds; the last character places it in Chinnock's "Lanceolata type" (Chinnock, 1975).

AIZOACEAE

Tetragonia L.

Although studies using fresh material are particularly desirable in this family, after examining the range of dried specimens at Kew I cannot believe that the plant called *Tetragonia implexicoma* (Miq.) Hooker f. is a different species from the New Zealand *T. trigyna* Banks & Sol. ex Hooker f. Even though the latter name was maintained by Allan (1961), Cheeseman (1914), in the text accompanying his excellent plate of *T. trigyna,* cast doubt on the distinctness of the two species. More recently, Sykes (1977, p. 75) also admitted that they are "very closely related." I therefore treat the Norfolk Island and Lord Howe Island plants as *T. implexicoma* (Miq.) Hooker f. (not "*amplexicoma,*" a typographic error that Miquel subsequently corrected). I have seen two collections, *McComish 52* (K), from Norfolk Island, and *McComish 118* (K), from Lord Howe Island.

It may be worth noting that the type material of *Tetragonella implexicoma* Miq. (the basionym of *Tetragonia implexicoma*), a Preiss collection from Rottnest Island, Western Australia, with its narrowly oblong-elliptic (almost linear) leaves 3–6 mm wide, looks very different from material I have seen of the plant known by this name from Victoria, South Australia, and Tasmania.

The related *Tetragonia tetragonioides* (Pallas) Kuntze also occurs on both islands.

AMARANTHACEAE

Centrostachys aquatica (R. Br.) Wallich

Although Moquin-Tandon (1849) recorded this species from Norfolk Island, an error followed by Schinz (1934) and Backer (1949), Robert Brown in his protologue (1810) described both *Achyranthes arborescens* and *A. aquatica* (the basionym of *Centrostachys aquatica*) "in obs." but attributed only the former to Norfolk Island.

EUPHORBIACEAE

Drypetes Vahl

The Lord Howe representative of this genus, which has been called *Drypetes affinis* Pax & Hoffm., is too close to *D. lasiogyna* (F. Mueller) Pax & Hoffm. of Australia to be specifically distinct, and I believe it should be reduced to a subspecies of the latter. They differ in fruit size (10–14 mm long in the Australian subsp. *lasiogyna* material, vs. 20–25 mm in subsp. *affinis* from Lord Howe) and in leaf texture and size (the Lord Howe plants have more coriaceous and usually slightly smaller leaves).

Two varieties of *Drypetes lasiogyna* subsp. *lasiogyna* have been recognized; their distributions adjoin in Queensland. They differ only in the indumentum of the ovary and fruit—hairy in var. *lasiogyna* and glabrous in var. *australasica* (Muell. Arg.) Airy Shaw. The Lord Howe Island plant has glabrous ovaries and fruits.

Drypetes lasiogyna (F. Mueller) Pax & Hoffm. subsp. **affinis** (Pax & Hoffm.) P. S. Green, comb. et stat. nov.

D. affinis Pax & Hoffm. *in* Engler, Pflanzenr. IV. **147 XV**(Heft 81): 271. 1922. TYPE: Lord Howe Island, "F. Mueller" (B, destroyed).
Hemicyclia sepiaria sensu F. Mueller, Fragm. Phytogr. Austral. **9:** 77. 1875.
H. australasica sensu Bentham, Fl. Austral. **6:** 118. 1873, *pro parte*; *sensu* Hemsley, Ann. Bot. **10:** 250. 1896; *sensu* Maiden, Proc. Linn. Soc. New South Wales **23:** 134. 1898; *sensu* Oliver, Trans. & Proc. New Zealand Inst. **49:** 141. 1917.
Drypetes lasiogyna (F. Mueller) Pax & Hoffm. var. *australasica* sensu Rodd & Pickard, Cunninghamia **1:** 272. 1983.

SPECIMENS EXAMINED. **Lord Howe Island**: SE lower slopes of Malabar, *Green 1572* (A, K); Ned's Beach, *Rodd 1426* (K), *Van Balgooy 1108* (K); on top of cliff at E end of Ned's Beach, *Uhe 1252* (K), *1264* (K); without further locality, *Milne 7* (K), *Moore 39* (K), *46* (K).

MORACEAE

Ficus L.

Although Corner (1965) reduced *Ficus columnaris* C. Moore & F. Mueller of Lord Howe Island to synonymy under *F. macrophylla* Desf. ex Pers. and determined the Kew isotype of the former as this species, I suspect that he did not see sufficient material to enable him to assess its real status.

The most remarkable characteristic of the Lord Howe Island plant is the lack of a single main trunk. Instead, it has ten to twenty or more trunks, many of them equally large, each having arisen from an aerial root that has reached down from a spreading canopy branch to touch the ground, root, and thicken into a stem with the dimensions of a trunk—hence the epithet *columnaris*. (Hutchinson (1969) published a sketch of the habit based on a drawing by C. Moore dated Aug. 1869, which accompanies the isotype of *Ficus columnaris* at Kew.) Duff (1882) recorded that the largest of the old trees were then reported

to cover an area of two to three acres (ca. 1 ha). This habit contrasts strongly with that of the mainland *F. macrophylla*, the Moreton Bay fig, which invariably has a single trunk with only limited development of banyanlike roots (these never attain the dimensions of a main trunk).

In addition the leaves of the Lord Howe Island plant have a strongly ferruginous indumentum on the undersides (vs. "finely white felted beneath, at first" for *Ficus macrophylla*—Corner, 1965, p. 109). On the island, even at a distance, the fig can be identified when the wind is blowing by the brown undersides of the leaves, a fact pointed out by C. Moore (1869a, 1869b), who also claimed that the island plant differed from *F. macrophylla* in the size of its fruits and leaves. From the limited material currently available (seven fruiting and eleven vegetative specimens in all), the possible differential character of fruit size does not seem very strong, although it may exist—the fruits on the two Lord Howe Island specimens in fruit are 15 mm long (vs. 16–19 mm for those of *F. macrophylla*). In leaf size there is considerable overlap: those of the former are 8–17.5 cm long, and those of the latter 10–21 cm.

Taking into account the habit and leaf indumentum, weakly supported by leaf and fruit size, I believe that the Lord Howe Island fig is worthy of recognition as a separate endemic subspecies.

Ficus macrophylla Desf. ex Pers. subsp. **columnaris** (C. Moore) P. S. Green, comb. et stat. nov.

F. columnaris C. Moore, Trans. Bot. Soc. Edinburgh **10:** 368. 1870, Official Visit Lord Howe Is. 1870, 21. 1870; C. Moore & F. Mueller, Proc. Acclim. Soc. Victoria **3:** 71. 1874, *in* F. Mueller, Fragm. Phytogr. Austral. **8:** 247. 1874. TYPE: Lord Howe Island, 1869, *C. Moore 56* (holotype, MEL, not seen; isotype, K!).

Although the date of publication of *Ficus columnaris* has usually been given as 1874, there seems to be no reason not to accept Moore's use of the name four years earlier. It was not published as provisional, and although the description is scanty by modern standards, it is adequate to establish valid publication.

The trees on Lord Howe Island seem to be susceptible to exposure and wind; the more the surrounding woody vegetation is removed and the figs isolated, the less they will thrive or even survive.

Malaisia Blanco

Malaisia scandens (Lour.) Planchon is the only species in this genus. Its distribution ranges from southern China and southeastern Asia through Malesia (including the Philippine Islands) to the Mariana Islands (*fide* Smith, 1981), Fiji, Tonga (*fide* Smith, 1981), New Caledonia, and Australia (coastal New South Wales, Queensland, and Northern Territory). Throughout this area the species appears fairly uniform, although several taxa have been described in the past.

However, the Lord Howe Island plant, isolated on a small oceanic island at the edge of the range of the species, differs consistently in leaf shape and fruit size from the rest of the specimens seen. The leaves are ovate or ovate-lan-

ceolate, (5–)8–11(–17) cm long, and consistently long-acuminate to acute (vs. rounded, acute, or abruptly acuminate at the apex). The mature fruits of the species as a whole vary in length from 6 to 8 cm, but those from Lord Howe Island are almost double this—13–14 cm long—and proportionately broad. Although Bentham had seen no carpellate or fruiting material, he noted (1873, p. 180) that the Lord Howe Island plant had "large ovate-acuminate or ovate-lanceolate leaves and remarkably large male spikes." Indeed, the staminate catkins are stouter and generally longer than those on specimens from the Australian mainland, and usually (but not always) larger than those on Malesian material.

The differences in leaf shape and fruit size, however, lead me to recognize the Lord Howe plant as an endemic subspecies.

Malaisia scandens (Lour.) Planchon subsp. **megacarpa** P. S. Green, subsp. nov.

A subsp. scandente foliis ovato-lanceolatis longe acuminatis, et fructibus majoribus (13–14 cm longis), differt.

TYPE. Lord Howe Island, Nov. 1938, *McComish 35* (holotype, K!).

MYRSINACEAE

Rapanea Aublet

Although Allan (1961) followed Hosaka (1940) in including *Rapanea* Aublet in *Myrsine* L., I prefer to follow Degener (1939), Oliver (1951), and Smith (1973) and maintain them as distinct genera, while agreeing that *Suttonia* A. Rich. is a synonym. The staminal "flange" typical of *Myrsine* is not present in *Rapanea.*

This is a difficult genus and is in need of revision. Although a number of the Pacific species have been sorted out by Smith (1973), those from Australia and the parts of Melanesia he did not cover are in need of critical study and assessment. Nevertheless, careful examination of the three species that have been described from Lord Howe Island (*Rapanea mccomishii* Sprague, *R. myrtillina* Mez, and *R. platystigma* Mez) shows them to be distinct and endemic to the island. The affinities of each of them, whether with Queensland, New Caledonia, Fiji, or New Zealand (*R. australis* (A. Rich.) W. Oliver), will need to be assessed when the Old World species have been revised.

The Norfolk Island species, an endemic known on the island as "beech," needs a new name because *R. crassifolia* R. Br. of Australia (with the type from Queensland) has been incorrectly used for it.

Rapanea ralstoniae P. S. Green, nom. nov.

Myrsine crassifolia sensu Endl. Prodr. Fl. Norfolk. 48. 1833; DC. Prodr. Syst. Nat. Regni Veg. **8:** 96. 1844, *pro parte*; Seem. Fl. Vit. 149. 1866; *non* R. Br.

Rapanea crassifolia sensu Mez *in* Engler, Pflanzenr. IV. **236**(Heft 9): 365. 1902, *quoad pl. ins. Norfolk.*; Maiden, Proc. Linn. Soc. New South Wales **28:** 707. 1904; Laing, Trans. & Proc. New Zealand Inst. **47:** 33. 1915; Turner *et al.* Conserv. Norfolk Is. 35. 1968; *non* (R. Br.) Mez.

SPECIMENS EXAMINED. **Norfolk Island:** in skirts of woods in shady spots, *Cunningham 18* (K); margin of woods, *Cunningham 95* (K); Mt. Bates, toward Red Road, low forest, *Green 1389* (A); Cook's Memorial, *Henderson s.n.,* 1967 (E); Anson Bay road, near Selwyn Bridge above Jacobs Rock, volcanic forested slopes, *Lazarides 8058* (K); ca. 2 mi [3.2 km] NE of cemetery at Kingston, *Uhe 1104* (K); top and upper slopes of Mt. Pitt, *Uhe 1156* (K), *1171* (K), *1180* (K); without further locality, *Backhouse 690* (K), *Bauer s.n.* (K), *Caley s.n.* (BM), *Cunningham s.n.,* 1830 (K), *Maiden & Boorman s.n.,* Nov. 1902 (BM, K), *Robinson s.n.,* 1902 (BM).

Bentham (1868) noted that the Norfolk Island and Australian plants were different. However, Mez (1902) cited *Rapanea crassifolia* in his monograph under both *R. subsessilis* (F. Mueller) Mez and *R. porosa* (F. Mueller) Mez. If those species remain distinct after revision, the type of *Myrsine crassifolia* R. Br. (*Rapanea crassifolia* (R. Br.) Mez) probably belongs to the latter and *R. porosa* will then pass into synonymy. I have seen the type of Robert Brown's species at BM.

It gives me great pleasure to name this Norfolk Island endemic after Mrs. Pat Ralston, who tragically died of cancer in 1971. During her lifetime she did much to revive an interest in the plants of Norfolk Island. Her anxiety at the destruction of the limited natural vegetation remaining on the island and her efforts to preserve it eventually led to the investigation carried out by Professor John Turner and colleagues on behalf of the Australian Conservation Foundation. This gave rise to their excellent publication, *The Conservation of Norfolk Island* (Turner *et al.,* 1968).

NYCTAGINACEAE

Pisonia L.

Sykes (1977, p. 121) has suggested that the "tropical" *Pisonia umbellifera* J. R. & G. Forster is different from the "homogeneous entity from Norfolk Island, the Kermadecs, and New Zealand." I agree, and with this entity I also include the plants from Lord Howe Island and Hawaii. The specific concept of Stemmerik (1964) has, in this case, been too broad, although he appears to have been correct in treating *Ceodes* J. R. & G. Forster, *Calpidia* Thouars, *Heimerlia* Skottsb., and *Heimerliodendron* Skottsb. as congeneric.

Pisonia brunoniana Endl. Prodr. Fl. Norfolk. 43. 1833; Maiden, Proc. Linn. Soc. New South Wales **28:** 712. 1903; Laing, Trans. & Proc. New Zealand Inst. **47:** 26. 1915; Oliver, Trans. & Proc. New Zealand Inst. **49:** 136. 1917. TYPE: Norfolk Island, *Bauer s.n.* (holotype, W, destroyed; isotype, K!).

Pisonia umbellifera sensu Hemsley, Ann. Bot. (London) **10:** 248. 1896; *sensu* Stemmerik, Blumea **12:** 280. 1964; *sensu* Turner *et al.* Conserv. Norfolk Is. 33. 1968.
Calpidia brunoniana (Endl.) Heimerl, Oesterr. Bot. Z. **63:** 283. 1913.
Ceodes brunoniana (Endl.) Skottsb. Svensk Bot. Tidskr. **30:** 738. 1936.
Heimerlia brunoniana (Endl.) Skottsb. *ibid.* 738. 1936.
Heimerliodendron brunoniana (Endl.) Skottsb. *ibid.* **35:** 364. 1941.

ORCHIDACEAE

In addition to his work on the orchids of Australia, Mark Clements, of the Australian National Botanic Gardens, Canberra, has studied those from Lord Howe and Norfolk islands and their relationships. As a result of these studies, including an examination of the types where indicated below, he has been able to provide the taxonomy and synonymy that follow; the nomenclatural conclusions, however, are my own.

Dendrobium Sw.

Until 1975, when the old Article 71 was deleted from the International Code of Botanical Nomenclature at the Leningrad International Botanical Congress, scientific names based on monstrosities could be rejected. However, this article is no longer a part of the Code, and the names of the *Dendrobium* plants from Norfolk Island with peloric flowers, named and described by Endlicher as early as 1833, can therefore no longer be rejected and must now be accepted as legitimate. It seems possible that the Norfolk Island populations, which appear to be permanently peloric, are apomictic. The legitimacy of names based on "monstrosities," along with the taxonomic conclusions that Clements reached after studying material from the islands and the mainland, affects the name of the well-known and widespread Australian plant *D. gracilicaule* F. Mueller, as follows.

Dendrobium macropus (Endl.) Reichb. f. ex Lindley, J. Linn. Soc., Bot. **3:** 9. 1859.

Thelychiton macropus Endl. Prodr. Fl. Norfolk. 33. 1833. TYPE: Norfolk Island, *Bauer s.n.* (w, not seen), *Bauer* icon. ("iconotype," w!).

Dendrobium macropus subsp. **gracilicaule** (F. Mueller) P. S. Green, comb. et stat. nov.

Dendrobium elongatum A. Cunn. Edward's Bot. Reg. **25:** Misc. 33. 1839; *non* Lindley, 1830.
D. gracilicaule F. Mueller, Fragm. Phytogr. Austral. **1:** 179. 1859. TYPE: Australia, Queensland, Moreton Bay, *F. Mueller s.n.* (MEL, not seen).

This subspecies grows in coastal New South Wales and eastern Queensland.

Dendrobium macropus subsp. **howeanum** (Maiden) P. S. Green, comb. et stat. nov.

Dendrobium gracilicaule F. Mueller var. *howeanum* Maiden, Proc. Linn. Soc. New South Wales **24:** 382. 1899. TYPE: Lord Howe Island, *Maiden s.n.* (NSW, not seen).

SPECIMENS EXAMINED. **Lord Howe Island:** ridge between Old Settlement and North Bay, *Green 1943* (K); ridge W of Malabar, *Green 1958* (K); last part of ascent of Mt. Gower, *Green 1609* (A); without further locality, [*Fullager*] *s.n.* (K), *MacGillivray* in *H.M.S. Herald Bot. 725* (K), *McComish 17* (K), *Milne s.n.*, Sept. 1853 (K).

This subspecies passes under a number of names on several southwestern Pacific islands. For example, it also occurs on New Caledonia (under *D. gracilicaule* F. Mueller; see Hallé, 1977) and Fiji (as *D. gracilicaule* var. *vitiense* Rolfe). It is conspecific with but sufficiently distinct—by virtue of its shorter, stouter inflorescences and its unspotted flowers (rarely with a few marks)—from subsp. *gracilicaule* on the mainland of Australia, which we believe to be closely related.

Dendrobium macropus subsp. **macropus**

Thelychiton brachypus Endl. Prodr. Fl. Norfolk. 33. 1833. TYPE: Norfolk Island, *Bauer s.n.* (W, not seen), *Bauer* icon. ("iconotype," W!).

SPECIMENS EXAMINED. **Norfolk Island:** N slopes of Mt. Bates, *Green 1422* (A); without further locality, *Backhouse 627* (K), *Laing s.n.* (CANTY), *McComish 75* (K). Sketch from Bauer drawing of *D. brachypus* (K).

I believe that the plant Endlicher called *Thelychiton brachypus* was a young specimen of this subspecies flowering before the canelike stem characteristic of the species had developed.

Microtis R. Br.

The earliest name applied to the one species of this genus growing on Norfolk and Lord Howe islands is given here.

Microtis unifolia (Forster f.) Reichb. f. Beitr. Syst. Pl. 62. 1871.

Ophrys unifolia Forster f. Fl. Ins. Austral. Prodr. 59. 1786. TYPE: New Zealand, *Forster s.n.* (BM?, not seen).
Epipactis porrifolia Sw. Kongl. Vetensk. Acad. Nya Handl. **21:** 233. 1800. TYPE: *Swartz*? (S, not seen).
Microtis porrifolia (Sw.) R. Br. Prodr. Fl. Novae Holland. 320. 1810.

SPECIMENS EXAMINED. **Lord Howe Island:** SE slope of Malabar, *Green 1556* (A); Transit Hill and Poole's Lookout, *McComish 20* (K); without further locality, *Fullager s.n.* (K). **Norfolk Island:** without further locality, *McComish 40* (K).

This species is also known from New Zealand and the Kermadec Islands, Australia, New Caledonia, and Vanuatu.

Oberonia Lindley

Although Dockrill (1966) treated the species from Norfolk Island and that from Australia as different and maintained the name *Oberonia palmicola* F. Mueller for the latter, he did not say how they differ and gave no reason for separating them. McGillivray (1969, p. 166) stated that "*O. palmicola* has been reinstated [as different from *O. titania*]," but he, too, have no reasons and just referred back to Dockrill (1966).

A careful examination of the type materials, including the excellent drawings by Ferdinand Bauer at Vienna, shows them to be the same.

Oberonia titania Lindley, Folia Orchid. *Oberonia* 8. 1859. Type as for *Titania miniata* Endl.

Titania miniata Endl. Prodr. Fl. Norfolk. 31. 1833; non *Oberonia miniata* Lindley (1843). TYPE: Norfolk Island, Anson Bay, *Bauer s.n.* (W!).
Oberonia palmicola F. Mueller, Fragm. Phytogr. Austral. **2:** 24. 1860. TYPE: Australia, New South Wales, *Beckler s.n.* (holotype, MEL, not seen; isotype, K!).

ADDITIONAL SPECIMENS EXAMINED. **Norfolk Island:** Mt. Bates track, *Ralston, Hoogland, & Turner s.n.*, 3 Oct. 1967 (K). Also, a dried specimen has been placed in the Kew Herbarium from a plant cultivated at Kew (8 Aug. 1972, Accession No. 310-71.02700) from *Green 1901,* collected on south slopes of Mt. Bates, 26 Aug. 1971.

Phreatia Lindley

Phreatia tahitensis Lindley, J. Linn. Soc., Bot. **3:** 62. 1858. TYPE: Tahiti, *Bidwill s.n.* (holotype, K-L!).

ADDITIONAL SPECIMENS EXAMINED. **Norfolk Island:** top of Mt. Bates, *Ralston 25* (A); without further locality, *Laing*(?) *s.n.* (CANTY), *McComish 144* (K).

This species has now been collected at least three times and is clearly indigenous. It has variously been identified as *Phreatia resiana* J. J. Smith and *P. obtusa* Schltr., but the latter is a synonym of *P. tahitensis* Lindley. On the island there is also *P. limenophylax* (Endl.) Bentham.

Taeniophyllum Bl.

This diminutive orchid was not discovered on Norfolk Island until 1967. It was then identified as *Taeniophyllum muelleri* Lindley ex Bentham, a species from Queensland. However, a careful comparison of the type of this species at Kew with *Ralston, Hoogland, & Turner s.n.*, 31 Oct. 1967, has shown that the latter is not the species from the Australian mainland. *Ralston et al.* is near the widespread Pacific *T. fasciola* (Forster f.) Reichb. f., but it is more diminutive and its flowers bear a smaller spur. It needs further study and may be an undescribed taxon.

POLYGONACEAE

Muehlenbeckia Meissner

The identity of the *Muehlenbeckia* on Lord Howe Island appears to have been in doubt. Although it has been recorded as *M. axillaris* (Hooker f.) Walp. by Bentham (1870) and subsequently by Mueller (1875), Hemsley (1896), Maiden (1898), and Oliver (1917), its correct identification has been queried. Rodd (1974) recorded it as *M. complexa* (A. Cunn.) Meissner, and Rodd and Pickard (1983) listed it as *Muehlenbeckia* cf. *complexa.*

After examining several collections from Lord Howe Island (*Fullager s.n., Green 1539, McComish 45, Moore 8, Rodd 1490, Uhe 1248,* and *Van Balgooy 1046*), I have concluded that the species represented there is indeed the New Zealand *Muehlenbeckia complexa* (A. Cunn.) Meissner.

SAPOTACEAE

Planchonella Pierre

Although Allan (1961) used the name *Planchonella novo-zelandica* (F. Mueller) Allan for the New Zealand member of this genus, I believe that it and the Norfolk Island representative are conspecific—a conclusion also reached by W. R. Sykes (pers. comm.) of New Zealand and alluded to by Smith (1981).

Planchonella costata (Endl.) Pierre ex H. J. Lam, Blumea **5:** 5. 1942.

Achras costata Endl. Prodr. Fl. Norfolk. 49. 1833. TYPE: Norfolk Island, *Bauer s.n.* (isotype, K!).
A. novo-zelandica F. Mueller, Fragm. Phytogr. Austral. **9:** 72. 1875. TYPES: New Zealand, *Colenso s.n.* (syntype, MEL?, not seen); *Kirk s.n.* (isosyntype, K!).
Planchonella novo-zelandica (F. Mueller) Allan, Fl. New Zealand **1:** 539. 1961.

ADDITIONAL SPECIMENS EXAMINED. **New Zealand:** between Ngaire and Wainai, opposite Cavallos, *R. Cunningham 404* (K); Whangarei Heads, "*Pickmere*" *13* (K); Kaikoura Is., *Kirk 70* (K); Kawau, *Kirk s.n.*, March 1868 (K); Little Barrier Is., *Shakespear s.n.* (K); Great and Little Barrier Is., *Kirk 70* (K); Manukau Heads, *Cheeseman 94* (K). **Norfolk Island:** upper slopes of Mt. Pitt, along Mt. Pitt Road, *Hoogland 11355* (K); without further locality, *Backhouse 615* (K), *A. Cunningham 20* (K), *96* (K), *Laing s.n.* (CANTY), *McComish 59* (K), *59A* (K).

Lam (1942) and Van Royen (1957) have recognized various varieties within their broad concept of *Planchonella costata,* but like Smith (1981) I believe that these represent other species.

Even though F. Mueller described the Lord Howe Island representative as distinct, examination of the range of material now available shows that it is conspecific with a species from the Australian mainland.

Planchonella myrsinoides (A. Cunn. ex Bentham) Blake & Francis, Austral. Rainf. Trees, ed. 2. 358. 1951.

Achras myrsinoides A. Cunn. ex Bentham, Fl. Austral. **4:** 283. 1869. TYPE: Australia, Queensland, Rodd's Bay, *A. Cunningham 123* (lectotype, K!, here designated).
A. howeana F. Mueller, Fragm. Phytogr. Austral. **9:** 72. 1875. ISOSYNTYPES: Lord Howe Island, *Fullager s.n.* (K!), *Milne 15* (K!), *Moore 37* (K!).
Planchonella howeana (F. Mueller) Pierre, Not. Bot. Sapot. 36. 1890.

ADDITIONAL SPECIMENS EXAMINED. **Australia.** QUEENSLAND. Cook Distr.: State Forest Reserve 607, Bridle Logging Area, 17°00'S, 145°35'E, *Hyland 7120* (K). Port Curtis Distr.: near Rockhampton, *Francis s.n.*, March 1920 (K). Burnett Distr.: Mt. Perry (inland from Bundaberg), *Boorman s.n.*, Aug. 1912 (K). Wide Bay Distr.: Imbil, *L. S. Smith & Webb 3133* (K); The Hummocks, ca. 5 mi [8 km] E of Bundaberg, *L. S. Smith 4103* (K). Moreton Bay Distr.: Brisbane R., *A. Cunningham 54* (K), *55* (K), *Fraser 192* (K). Without further locality: Queensland woods, London Exhibition of 1862, *Hill 49* (K). NEW SOUTH WALES: Sydney woods, Paris Exhibition of 1854, *C. Moore 27* (K), *40* (K). **Lord Howe Island:** E side of Intermediate Hill, *Game 69/009* (K); Transit Hill, *Van Balgooy 1006* (K); ridge between Old Settlement and North Bay, *Green 1926* (K); on top of cliff at E end of Ned's Beach, *Uhe 1253* (K).

Bentham (1868) referred the Lord Howe Island plant to *Achras australe* R. Br. (*Planchonella australis* (R. Br.) Pierre), but this is quite a different species.

Although I have not seen the type, I strongly suspect that *Planchonella reticulata* (Baillon) Pierre, described from New Caledonia, is also a synonym of *P. myrsinoides.* Van Royen (1957) cited a Lord Howe Island collection under this otherwise New Caledonian species. However, with the material at hand at Kew, it is impossible to be positive that the two are conspecific.

ULMACEAE

Celtis L.

Celtis paniculata (Endl.) Planchon, Ann. Sci. Nat. Bot. III. **10:** 305. 1848.

Soepadmo (1977) has lumped too enthusiastically, and I agree with A. C. Smith (1978, 1981) that he has included in *Celtis paniculata* taxa that should be maintained as distinct.

The correct name for the Norfolk Island plant is in no doubt, for that island is the type locality of the species. However, when the geographic relationships of the flora of Norfolk Island are considered, it will be necessary to identify the true range of *Celtis paniculata* sensu stricto.

Typical *Celtis paniculata* also seems to occur in New Caledonia (along with other species of the genus) and Australia (northeastern New South Wales and coastal Queensland, including islands in the Gulf of Carpentaria), yet not on Lord Howe Island.

The Fijian plants, *Celtis harperi* Horne ex Baker and *C. vitiensis* A. C. Smith, as Smith (1978, 1981) has pointed out, are distinct from *C. paniculata* in a number of morphological characters that he detailed. I agree also that the plants from farther east, into Polynesia, are different yet again (*C. pacifica* Planchon); those from Tonga and Niue (see Sykes, 1970) are *C. harperi.*

The leaves on the specimens I have seen from New Guinea, Borneo, the Solomon Islands, and Micronesia, although close (especially in venation) to those of *Celtis paniculata,* are consistently elliptic (not ovate-lanceolate) with an acute, rarely subacuminate, apex, not long-acuminate and narrowly acute as in the Norfolk Island plants. The fruits, too, are clearly smaller (5–6 mm long vs. 10–11 mm) and distinctly beaked (with more prominent stylar arms); the inflorescences are somewhat strigose, in contrast to glabrous in typical *C. paniculata.* The specimens at Kew from the Moluccas, Ceram, and Tanimbar seem, however, to be *C. paniculata* sensu stricto, or intermediates. A critical and careful study of this complex throughout its range is needed. When this is carried out, I suspect that some of the entities just mentioned will be recognized as subspecies of *C. paniculata.*

There is no doubt that *Celtis conferta* Planchon (both var. *cuneata* Planchon and var. *elliptica* Planchon, which I do not consider sufficiently different for separate recognition) from New Caledonia (Planchon, 1873) is very close to the *Celtis* from Lord Howe Island. They both have elliptic leaves with rounded

apices, short petioles, and venation that is impressed above, giving a slightly bullate appearance; both also have dense inflorescences.

There are differences between the plants from the two islands, however, even though some characters overlap. The broadly conoid fruits from Lord Howe Island seem distinct, for although I cannot be sure that I have seen mature fruits of the New Caledonian plant, those on *McKee 3785* have a shrivelled mesocarp and a hard endocarp and appear to be at least nearly ripe. They are 4.5 mm long (plus a stylar beak 1 mm long), with the endocarp very shallowly pitted; those of *Vieillard 3150* are the same. This contrasts with the fruits on *McComish 111A* and *Uhe 1244* from Lord Howe Island, which are 6–7 mm long (plus a 1-mm stylar beak) and have deeply pitted endocarps 5.5–6 mm long.

The plant from New Caledonia also appears to have consistently smaller leaves that range from 2 to 6.5 cm (vs. 3–9 cm on the Lord Howe Island plant). The number of pinnate veins on each side of the midrib, above the strong basal lateral pair, is fewer in leaves from New Caledonia, but I believe this is directly related to leaf size, especially length.

Considering the differences and similarities together, I am convinced that the taxonomic situation is best reflected by treating these taxa from adjacent islands as subspecies. In view of the priority of Planchon's name, a new combination is needed for the Lord Howe Island plant.

Celtis conferta Planchon subsp. **amblyphylla** (F. Mueller) P. S. Green, comb. et stat. nov.

C. amblyphylla F. Mueller, Fragm. Phytogr. Austral. **9:** 76. 1875. TYPE: Lord Howe Island, *Moore & Fullager s.n.* (MEL, not seen; isotype, K!).

VIOLACEAE

Viola betonicifolia Smith subsp. **novo-guineensis** D. M. Moore, Feddes Repert. Spec. Nov. Regni Veg. **68:** 82. 1963.

The three collections of *Viola* from Norfolk Island that I have examined (*Backhouse s.n.,* 1835 (K), *Laing s.n.* (CANTY), and *McComish 51* (K)), as well as the living plant rediscovered during the Flora and Fauna Society field meeting on 28 August 1971, all agree with Moore's subspecies, which also occurs in eastern Queensland. In 1971 the plant was photographed but not collected so as not to endanger the population further, for the wild violet had not then been seen on the island for many years.

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NEW SPECIES AND NOTES ON LAURACEAE FROM THE CARIBBEAN LOWLANDS OF COSTA RICA

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In the summer of 1979, intensive collecting was begun toward a flora project for Finca La Selva, a biological field station managed by the Organization for Tropical Studies (OTS) in the Caribbean lowlands of northeastern Costa Rica. This area of approximately 1400 hectares is estimated to harbor at least 1500 species of vascular plants (Hammel & Grayum, 1982). Despite Costa Rica's history of intensive collecting (Prance, 1978), the entire Sarapiquí region, in which the La Selva field station lies, is still relatively unknown botanically (Gentry, 1978). Approximately 50 new species of flowering plants already have been or soon will be described from the station, most of them having come to light through intensive collecting for the flora project. Among these novelties are the four species of Lauraceae here described.

The Lauraceae are mostly tropical in distribution, and the family is particularly well represented in South America. Especially in the New World, revisionary work is sorely needed in order to determine generic limits. At the same time, many more collections and associated field observations are necessary to match fruits with flowers and to determine the variation within species. Eleven of the 17 New World genera are endemic, and 12 genera are known from Central America. The family contains between 2000 and 2500 species worldwide, with about 150 species in Central America (Allen, 1945). A total of 28 species in six genera (*Beilschmiedia* Nees, *Licaria* Aublet, *Nectandra* Rolander, *Ocotea* Aublet, *Persea* Miller, *Phoebe* Nees) are known from the La Selva field station. Eleven of these are also known from South America, and five—here discussed under "Additional Notes"—are shared with the West Indies.

Anyone attempting to identify Lauraceae in the Neotropics soon learns that under the prevailing taxonomy it is often difficult to identify specimens even to genus. This problem is due, in part, to the nature of the plants. They are usually tall trees with inconspicuous flowers, and most species are restricted to primary forest habitats where the individuals are often far apart. Many species are cryptically dioecious (both sexes have apparently "perfect" flowers), and most are seasonal; the fruits take several months to mature, so specimens rarely have both flowers and fruits. As a result, many species are known from few collections, and new species have often been described from incomplete

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material. Thus, the taxonomic references on which we rely are often based on little information.

In addition, characters such as anther-valve orientation, traditionally used to distinguish some genera, may be variable within certain species or even among flowers on an individual. Thus, many large genera as commonly diagnosed and identified are probably not monophyletic (see Kostermans, 1957). The history recorded in publications and on annotation labels demonstrates that even specialists with many years of experience in the family have difficulties. A comment of this sort is almost the standard preface to treatments of the Lauraceae (see Mez, 1889; Allen, 1945; Kostermans, 1952; Bernardi, 1962; Croat, 1978; Howard, 1981).

Given some field experience and herbarium study, many workers would probably agree that much would be gained by merging (at least conceptually) *Nectandra, Ocotea, Persea,* and *Phoebe* and simply sorting the species. On that basis we might begin to recognize any number of monophyletic supraspecific taxa. Particularly with regard to *Nectandra* and *Ocotea,* actual nomenclatural merger has been advocated (Kostermans, 1957) and, more recently, put into practice (Howard, 1981). However, for the few species at La Selva, the traditional generic distinctions are rather clear and appear to provide meaningful groupings of species. Thus, I choose to recognize the two genera, but for practical purposes in my treatment of the Lauraceae for the Flora of La Selva, I include the species together under one key, in which they are sorted without reference to generic characters.

The descriptions and observations presented in this paper are based on two years of field work at La Selva and examination of the Lauraceae holdings at CR, DUKE, F, NY, and US, as well as selected specimens from GH, LL, MICH, and MO.

NEW SPECIES

Licaria sarapiquensis Hammel, sp. nov. FIGURE 1.

Arbor 6–20 m. Folia alterna, elliptica, 15–20 × 5–7 cm, apice anguste acuminata, basi acuta, omnino glabra; supra atroviridia nitida. Paniculae sparsiflorae, ramis gracilibus, ramis ultimis umbelliformibus. Flores urceolati vel globosi, 2.3–2.5 mm longi, tepalis erectis vel incurvatis sub anthesi; antherae filamentis breviores, dehiscentia apicalis et extrorsa; glandulae claviformes, filamentis subaequilongae; staminodia ligulata tenuia, staminibus externa, filamentis subaequilonga. Fructus ovoideus, ca. 2 cm longus; cupula tenuiter duplomarginata.

Tree 6–20 m tall, 5–20 cm dbh; bark gray to nearly black, the inner bark thin, yellow, with strong, distinctive fragrance of sassafras. Leaves alternate; petiole 0.5–1 cm long; blade elliptic, 15–20 by 4.5–7 cm, the tip narrowly caudate, 1–3 cm long, the major lateral veins 5 to 7, arising at 50–75° angle, distinctly loop connected, the minor venation reticulate, prominent on both surfaces but more so below in dried material, the upper surface dark green, shiny, the lower surface dull, paler. Inflorescences paniculate, 2.5–4 cm long,

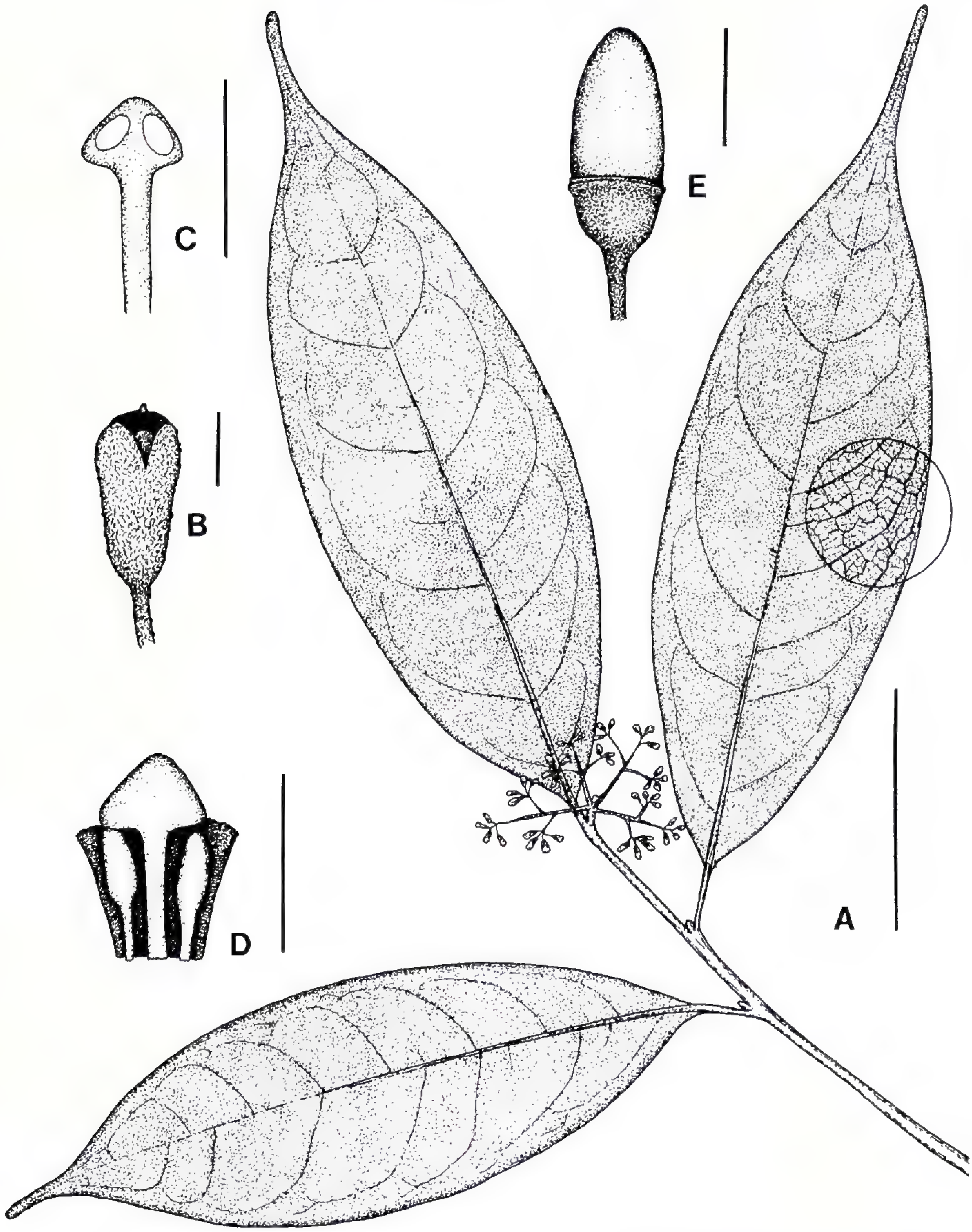

FIGURE 1. **Licaria sarapiquensis:** A, habit, scale = 5 cm; B, flower, scale = 1 mm; C, stamen, abaxial view, scale = 1 mm; D, stamen with basal glands on background of staminodia, adaxial view, scale = 1 mm; E, fruit, scale = 1 cm. (A from *Hammel 12235,* B–D from *Hammel 8663,* E from *Hammel 10532.*)

very slender branched and sparsely flowered, the ultimate clusters of flowers umbelloid, glabrous. Flowers urceolate to globose, 2.3–2.5 mm long, yellow-green, very inconspicuous; tepals ligulate, 1.2 mm long, about as long as floral tube, patent or curved inward at anthesis; inner 3 stamens fertile, 1.2 mm long, the anthers much shorter than filaments, oblate depressed, the valves opening

apically and somewhat extrorsely, the filaments 1 mm long, the glands stipitate, equaling filaments in length, with stipe as long as body of gland; outer 6 stamens sterile, membranous, ligulate; staminodia about same length as floral glands; ovary more or less pyriform, style and ovary together 1.8 mm long. Fruits ovoid-ellipsoid, 2 cm long, 0.8 cm in diameter, black at maturity, lower ⅓ covered by conical, thinly double-margined red cupule. Flowering in mid-May; fruits maturing in late August. Known only from Costa Rica.

TYPE. Costa Rica, Heredia, Finca La Selva, on Río Puerto Viejo just E of junction with Sarapiquí, elev. ca. 100 m, 14 May 1980, *Hammel 8663* (holotype, DUKE; isotypes, CR, DUKE, F, MO).

ADDITIONAL SPECIMENS EXAMINED. **Costa Rica.** HEREDIA: Finca La Selva, *Hammel 10532* (DUKE), *12235* (DUKE), *Hartshorn 1588* (CR).

Licaria Aublet is the only genus of Lauraceae in Central America with just three fertile stamens. It is also distinctive in having two rather than four valves per anther and a double-margined fruit cupule.

All of the flowering individuals of this species seen at La Selva were slender understory treelets about 6–12 m tall and 5–10 cm dbh. They often appeared dependent on nearby trees for support and were not observed to set fruit. The one fruiting individual found at La Selva (*Hammel 10532*) was a stout mid-canopy tree ca. 20 m tall. Although the flowers of the small individuals appeared to be perfect, these plants may be functionally staminate until reaching a certain size. The occurrence of a similar phenomenon has been verified for at least one species of Lauraceae; quantitative data from a large population of *Ocotea tenera* Mez at Monte Verde, Costa Rica, indicate a definite relationship between size and sex in this dioecious species (Wheelwright, pers. comm.).

The leaves of *Licaria sarapiquensis* are very distinctive in having long-acuminate tips and shiny, dark green upper surfaces (retained even in dried material). In this respect, as well as in details of the fruits, the species is remarkably similar to *L. armeniaca* (Nees) Kosterm., of South America. However, the tepals of *L. armeniaca* are much larger and reflexed, the filaments are indistinct from the anthers, and the floral glands are larger and tepaloid.

In Kostermans's (1937) treatment this new species would key to *Licaria pucheri* (Ruiz & Pavon) Kosterm., also of South America. However, the leaves of *L. pucheri* are not long acuminate, the basal glands are sessile and smaller, and the cupule margins are much wider than those of *L. sarapiquensis*.

This new species superficially resembles *Licaria guatemalensis* Lundell, but details of its leaves, flowers, and fruits suggest a closer relationship to the South American *L. armeniaca* than to any known Central American *Licaria*.

The epithet for this species is taken from the Sarapiquí region of Heredia Province, in which La Selva lies.

Nectandra hypoleuca Hammel, sp. nov. FIGURE 2.

Arbor 10–15 m. Folia elliptica 17–27 × 6.5–10 cm, apice acuminata, basi acuta, glabra, praeter subtus pilis in axillis nervorum costa et nervis planis vel leviter impressis, griseoviridia supra, glauca subtus. Stamina externa subses-

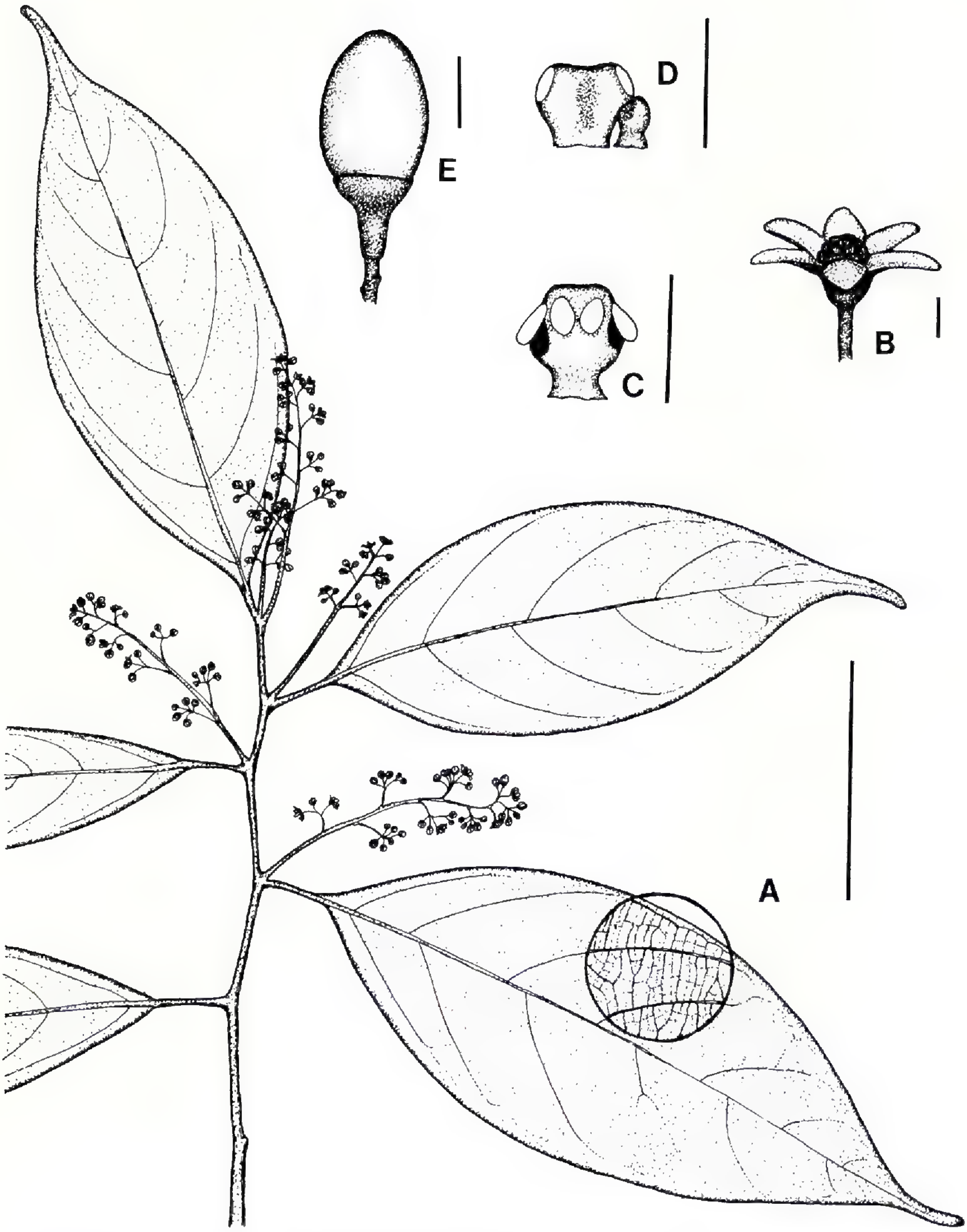

FIGURE 2. **Nectandra hypoleuca:** A, habit, scale = 5 cm; B, flower, scale = 1 mm; C, outer stamen, adaxial view, scale = 1 mm; D, inner stamen with staminodium, adaxial view, scale = 1 mm; E, fruit, scale = 1 cm. (A from *Hammel 9111,* B–D from *Hammel & Trainer 13074,* E from *McDowell 601.*)

siles, valvulis uniseriatis; staminodia 0.4 mm longa. Fructus ovoideus, 1.5–2.5 cm longus; cupula ca. 0.7 cm lata et alta.

Tree 5–15 m tall, 10–30 cm dbh; bark surface dark brown. Leaves with petiole 0.75–1.5 cm long; blade elliptic, 17–27 by 6.5–10 cm, the apex acuminate, the base acute, the midrib plane to somewhat impressed above, prom-

inent below, the major lateral veins 5 to 7, arising at 30–60° angle, plane or slightly impressed above, the upper surface dull, drying grayish green, glabrous, the lower surface usually glaucous and glabrous except for densely brown-pubescent domatia in vein axils. Inflorescences paniculate, axillary, clustered toward branch ends, 8–18 cm long, rachis sparsely pubescent. Flowers ca. 5 mm wide, sparsely pubescent; tepals ligulate, 2–2.4 mm long, spreading and bright white at anthesis; outer 6 stamens nearly sessile, quadrate, somewhat emarginate, 0.6–0.8 mm long, the anther valves arranged in low arc or horizontal line, outer 2 lateral; staminodia clavate, ca. 0.4 mm tall; ovary globose, ca. 0.6 mm long, style slightly shorter. Fruits ovoid, 1.5–2.5 cm long, 0.5 cm in diameter; cupule conical, ca. 0.7 cm tall, 0.7 cm in diameter. Flowering most commonly in June but also in early November; fruits maturing by October. Known only from Costa Rica.

TYPE. Costa Rica, Heredia, Finca La Selva, on Río Puerto Viejo just E of junction with Sarapiquí, elev. ca. 100 m, 23 June 1980, *Hammel 9111* (holotype, DUKE; isotypes, CAS, CR, F, MICH, MO, NY).

ADDITIONAL SPECIMENS EXAMINED. **Costa Rica.** HEREDIA: Finca La Selva, *Grayum 1482* (DUKE), *Hammel 8864* (DUKE), *10073* (DUKE), *10348* (DUKE), *Hammel & Trainer 12840* (DUKE), *12848* (DUKE), *13074* (DUKE), *Hartshorn 950* (CR), *1751* (CR), *McDowell 601* (DUKE).

This species has the outer six stamens each with four anther valves in a low arc or horizontal line, the tepals spreading or reflexed and ligulate, and the fruits with a definite cupule. Thus, it can be clearly placed within *Nectandra*.

Nectandra hypoleuca is known only from the La Selva field station, where it is frequent in the old secondary woods and alluvial forest along the Río Puerto Viejo. It can be recognized by its gray-green leaves, which are strikingly silvery-white (glaucous) below. This feature is particularly obvious on the leaves of saplings and in new leaves but is also present on mature ones. A sweet coconut fragrance perfumes the air when these plants burst into flower.

This new species is probably closely related to *Nectandra woodsoniana* Allen, of El Salvador, Costa Rica, and Panama, which differs primarily in its leaves that are not glaucous and that have the secondary and tertiary venation elevated on the upper surface, and its staminodia that are larger.

Bernardi (1967) placed *Nectandra woodsoniana* in synonymy under *N. martinicensis* Mez. With regard to the latter name, I have examined only the isotype at MO, *Sieber 99*. In addition to the above features, it differs markedly from *N. hypoleuca* in having shiny, conspicuously pellucid-punctate leaves.

The epithet for this new species refers to the white lower surface of the leaves.

Ocotea hartshorniana Hammel, sp. nov. FIGURE 3.

Arbor 20–30 m, radices gralliformes ferens. Folia oblonga, 12–19 × 3.5–7 cm, supra in medio latissima, apice abrupte acuminata, basi acuta lamina decurrenti, supra nitida, subtus pubescentia pilis erectis, glauca; costa basi latior; pubescentia ferruginea. Staminodia nulla. Fructus cylindricali-ovoideus, apiculatus, ca. 2 cm longus; cupula ca. 1.5 cm longa.

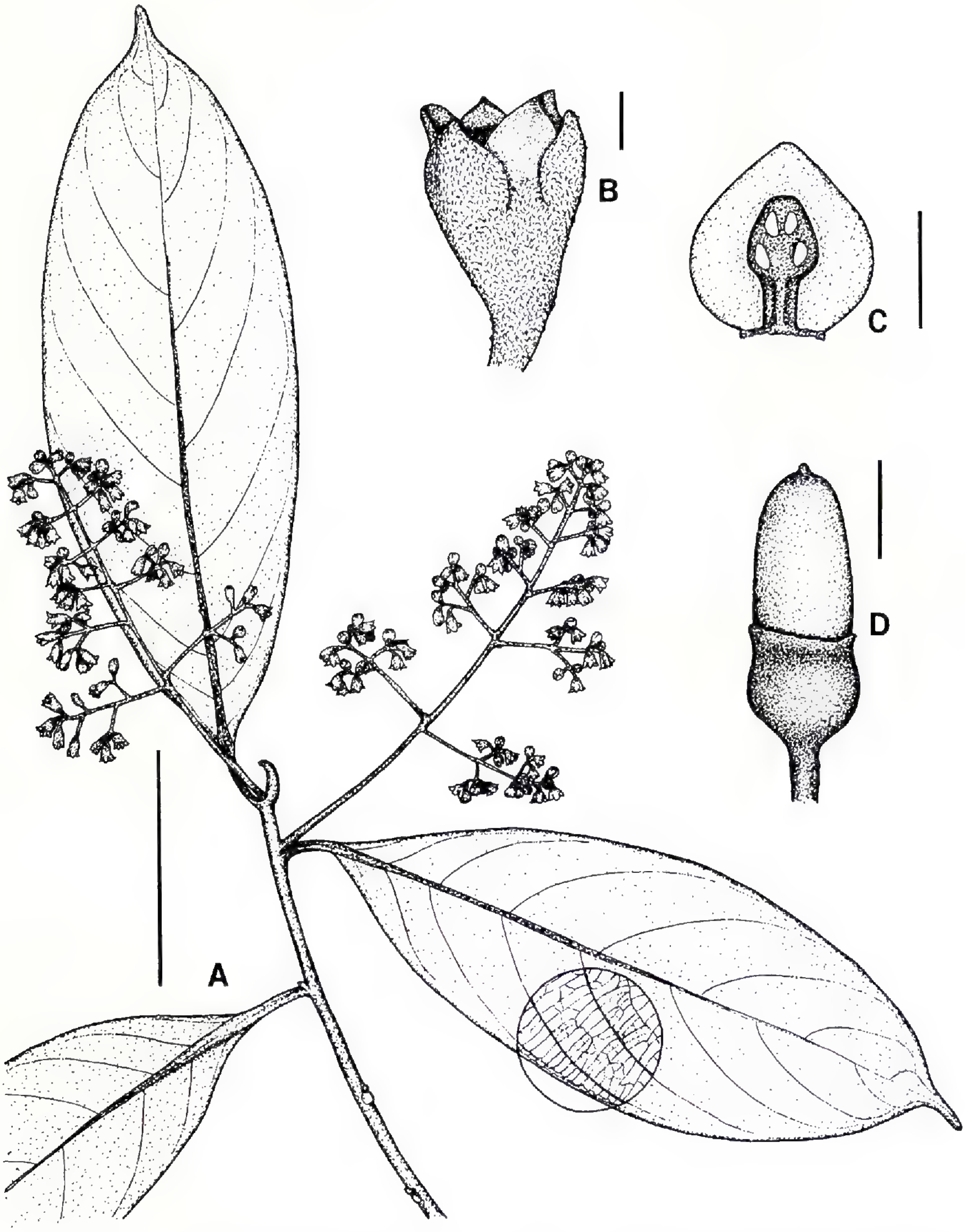

FIGURE 3. **Ocotea hartshorniana:** A, habit, scale = 5 cm; B, flower, scale = 1 mm; C, tepal and outer stamen, adaxial view, scale = 1 mm; D, fruit, scale = 1 cm. (All from *Hammel 11932*.)

Tree 20–30 m tall, 40–100 cm dbh; surface of bark pinkish tan, inner bark pink; trunk usually with stout adventitious roots. Leaves with petiole 0.5–1.5 cm long, flattened; blade obovate, 12–19 by 3.5–7 cm, the apex abruptly acuminate, the base acute, decurrent, the margin often slightly revolute, the midrib plane above, tomentulose, the lateral veins also plane or slightly impressed

above, rusty pubescent and prominent below, the tertiary venation reticulate and conspicuous on both surfaces, the major lateral veins usually 6 to 8, arising at 30–40° angle, the upper surface glabrous, shiny, the lower surface soft pubescent with erect hairs, glaucous (canopy leaves). Inflorescences axillary, paniculate, clustered among distal leaves, 12–15 cm long, densely flowered; rachis rusty pubescent. Flowers 3 mm long, rusty pubescent; tepals triangular, 1.6–2 mm long, erect at anthesis; outer stamens 1.2 mm long, the anthers triangular, slightly longer than pubescent filaments; staminodia lacking; ovary pyriform, narrowed at base, 1.5 mm tall, the style 1 mm long, the stigma peltate. Fruits ovoid-cylindrical, ca. 2 cm long, 1 cm in diameter, obtuse, apiculate, green at maturity; cupules urceolate, ca. 1.5 cm long, brownish, covering lower ⅓ of fruit. Flowering and fruiting April and May. Known from Costa Rica and Ecuador.

TYPE. Costa Rica, Heredia, Finca La Selva, on Río Puerto Viejo just E of junction with Sarapiquí, elev. ca. 100 m, 2 May 1982, *Hammel 11932* (holotype, DUKE; isotypes, CAS, CR, F, MICH, MO, NY, US).

ADDITIONAL SPECIMENS EXAMINED. **Costa Rica.** HEREDIA: Finca La Selva, *Folsom 9930* (DUKE), *Hammel 10630* (DUKE), *Hartshorn 1140* (MO), *1218* (MO), *1638* (MO), *Neil 5122* (DUKE, MO), *D. Smith 245* (DUKE). ALAJUELA: ca. 2 km S of Colonia Blanca, elev. 700–800 m, *Utley & Utley 5407* (DUKE). SAN JOSÉ: La Hondura, elev. 1300–1700 ft, *Standley 36330* (US); San Pedro de la Calabaza, elev. 1100 m, *Cooper 10330* (US). **Ecuador.** ESMERALDAS: Río Hoja Blanca con Río Hualpi, elev. 75 m, *Little & Dixon 21067* (US).

This species is placed in *Ocotea* because of its broadly triangular tepals that are erect at anthesis, its nine fertile stamens with the anther valves arranged in a narrow arc or two columns, and its fruit with a cupule.

At La Selva this species is quite conspicuous, although it is apparently restricted to the alluvial forest near the Río Puerto Viejo. Juvenile plants are common and are very distinctive because of their tiered growth form and their reddish orange new leaves with rusty-red pubescence. Mature plants usually have stout adventitious prop roots, apparently an unusual feature in the Lauraceae. This species does not appear to be dioecious; I observed no individuals that produced flowers but no fruits. The anthers of plants seen to produce fruits contained pollen.

Ocotea hartshorniana is probably closely related to *O. caracasana* (Nees) Mez (= *Nectandra hypoglauca* Standley ex Allen; holotype, Panama, *Davidson 531* (F!)), which also occurs at La Selva. Both have prop roots, and they are similar in details of venation, pubescence, flowers, and fruits. *Ocotea hartshorniana* differs primarily in its lack of staminodia and in its redder pubescence, which is more erect, especially on the lower surface of the leaf. A third species with prop roots, *O. mollifolia* Mez & Pittier ex Mez, of Costa Rica, is also known from La Selva and shares some features of pubescence, flowers, and fruits with the above two species. It differs in having shorter, unwinged petioles and broader leaves that are not glaucous below.

This new species is named to honor Gary Hartshorn, whose initial efforts and continued support toward uncovering the tremendous diversity of plants at La Selva provided the original basis and stimulus for the flora project.

Phoebe chavarriana Hammel, sp. nov. FIGURE 4.

Arbor 10–15 m. Folia alterna grandissima, elliptica, 25–50 × 10–23 cm, apice et basi acuta vel fere rotunda, omnino glabra, nervatura pinnata paribus nervorum ca. 8–10, subtus ut videtur glauca; petioli ca. 3.5–4.5 cm longi. Fructus ovoideus, ca. 1.5–1.8 cm longus; cupula tenuis vadosa.

Small tree 10–15 m tall, 15–25 cm dbh; surface of bark reddish brown, marked with long, horizontal lenticels, warty, the inner bark marbled tan and white, slowly oxidizing orange, very fragrant of avocado. Leaves with petiole (2–)3.5–4.5(–6) cm by 3–5 mm, channeled above, reddish; blade elliptic, 25–50 by 10–23 cm, usually slightly more than 2 times longer than wide, coriaceous, the base and apex acute to obtuse, the midrib impressed above, prominent below, the venation strictly pinnate, with the (6 to) 8 to 10 major lateral veins borne at 45–50° angle and as much as 4–5(–12) cm apart, the upper surface satiny, glabrous, the lower surface dull, much paler, appearing glaucous due to papillose epidermal cells, glabrous. Inflorescences paniculate, axillary, clustered near branch tips, 12–23 cm long; rachis nearly glabrous to sparsely short appressed pubescent. Flowers 2.5–3.2 mm long; nearly glabrous to sparsely appressed pubescent; tepals 2.3–2.4 mm long, greenish white, outer whorl as long as or slightly shorter than inner; outer stamens 1.7–1.9 mm long, the filaments ca. ½ length of anthers, sparsely pubescent; staminodia broadly cordate, 1.2 by 0.8–1 mm, stipitate, sparsely pubescent; ovary globose, equal in height to style, both glabrous. Fruits ovoid, 1.5–1.8 cm long, 1–1.2 cm in diameter, dark green to almost black at maturity; cupule thin, shallow, the margin lobed from persistent, accrescent tepals, the fruiting pedicel conical, 1–1.5 cm long, somewhat thickened, red. Flowering April and May; fruits maturing in late July. Known only from the Caribbean lowlands of Costa Rica.

TYPE. Costa Rica, Heredia, Finca La Selva, on Río Puerto Viejo just E of junction with Sarapiquí, elev. ca. 100 m, 2 May 1982, *Hammel 11931* (holotype, DUKE; isotypes, CR, F, MO).

ADDITIONAL SPECIMENS EXAMINED. **Costa Rica.** HEREDIA: Finca La Selva, *Grayum 2767* (DUKE), *Hammel 9287* (DUKE), *Hammel & Trainer 12922* (DUKE), *Hartshorn 1289* (CR); along Río Peje ca. 2 km S of Finca La Selva western annex, elev. ca. 150 m, *Hammel 11679* (DUKE).

This species is placed in the genus *Phoebe* because of its large, stipitate staminodia and its definite, although thin and shallow, fruit cupule.

Phoebe chavarriana is found scattered in primary forest at La Selva, most often on slopes and ridges. It has also been collected in primary forest along the Río Peje south of the La Selva property. Its extremely large, glabrous, pale green leaves distinguish this species from all other Lauraceae in the region. Although the leaves appear to be glaucous below, the effect is due to the refractive nature of the papillose epidermal cells rather than to any kind of waxy coating. The flowers of this species apparently lack fragrance at anthesis.

Although the flowers of *Phoebe chavarriana* are similar in detail to those of *Persea pallida* Mez & Pittier and *Persea rigens* Allen, the fruits are characteristic of the genus *Phoebe*. While fruits of *Persea* lack a cupule, those of *Phoebe*

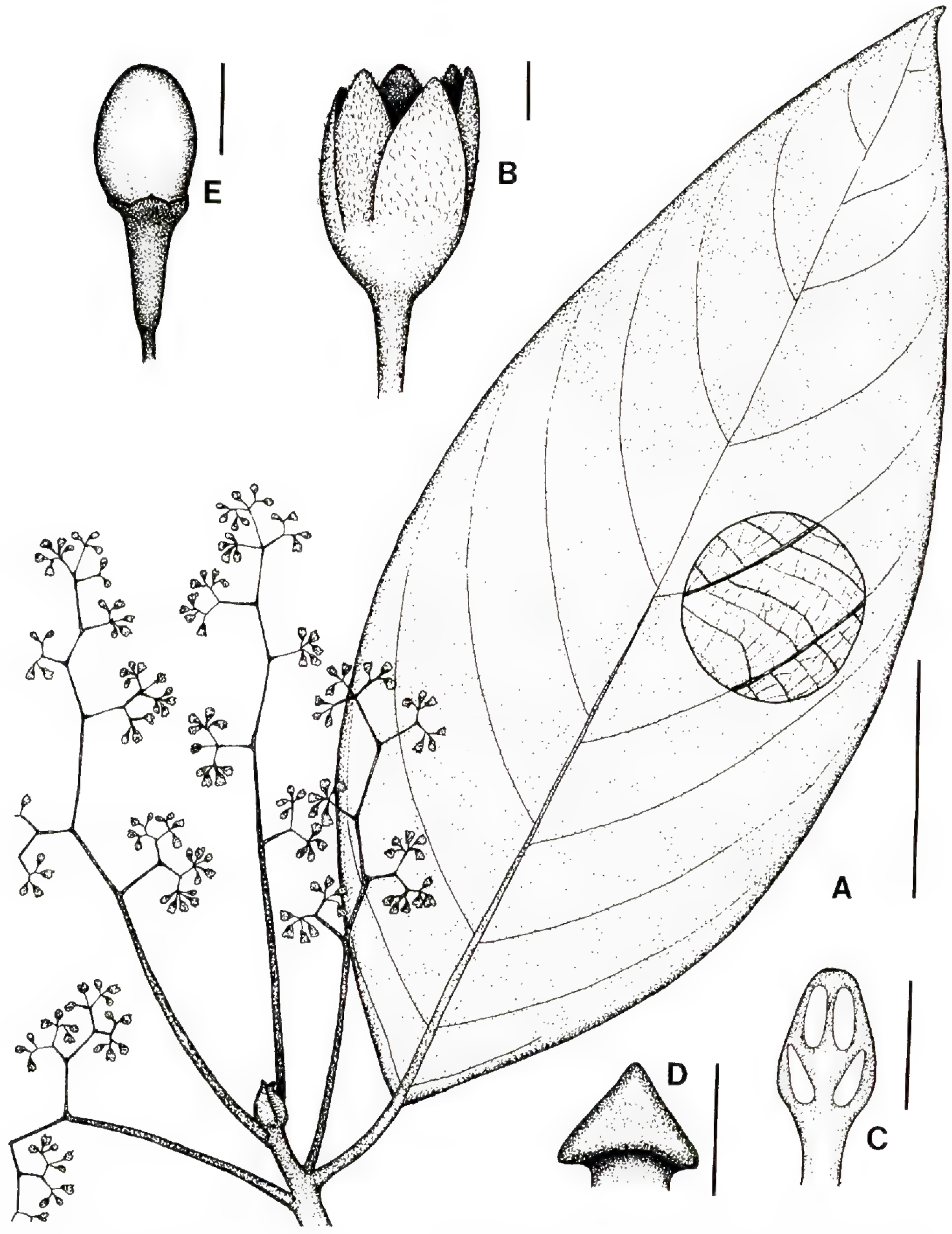

FIGURE 4. **Phoebe chavarriana:** A, habit, scale = 5 cm; B, flower, scale = 1 mm; C, outer stamen, adaxial view, scale = 1 mm; D, staminodium, scale = 1 mm; E, fruit, scale = 1 cm. (A from *Hammel 11931,* B–E from *Hammel 9287.*)

chavarriana are borne atop an enlarged, conical pedicel on a shallow cupule fringed by the persistent, accrescent tepals; they differ only in size from those of the widespread *Phoebe cinnamomum* (= *Phoebe mexicana* Meissner). Except for its subtriplinerved and smaller leaves, this latter species bears a strong resemblance to *P. chavarriana,* and the two are probably closely related.

This new species of *Phoebe* is named in memory of Rafael Chavarria, who

first came to the Sarapiquí lowlands on horseback and then to the forest by foot on trails where roads and bridges lie now. He worked for 20 years as foreman and boatman at Finca La Selva. Don Rafael was an ardent conservationist and loved the forest.

ADDITIONAL NOTES: AFFINITIES WITH WEST INDIAN PLANTS

All of the genera of Lauraceae at the La Selva field station also occur in the West Indies. In addition, the genus *Aniba,* which has been found very near La Selva and which was once thought restricted to the West Indies and South America, is here reported from Costa Rica and Panama. Five of the 28 species of Lauraceae found at the La Selva field station are also known from the West Indies. Bernardi (1967) has detailed the synonymy and the occurrence in Central America of one of these, *Nectandra membranacea* (Sw.) Griseb. The other four merit further discussion.

Aniba Aublet, Hist. Pl. Guiane Franç. **1:** 327, **2:** *t. 126.* 1775.

Although *Aniba* has previously been reported from Central America, the species involved have since been placed in other genera, and recently this genus has been considered restricted to the West Indies and South America (Kubitzki, 1982). However, collections from forest just a few kilometers south of the La Selva field station have revealed a new species of *Aniba,* probably related to *A. intermedia* (Meissner) Mez (Kubitzki, pers. comm.). A second species occurs in Darién province of Panama.

SPECIMENS EXAMINED. **Costa Rica.** HEREDIA: near Chilamate, Finca Bejuco, *Hammel 13366* (CR), *Hammel & Trainer 13111* (DUKE). **Panama.** DARIÉN: *Duke 4918* (NY), *13569* (NY), *Stern et al. 114* (NY), *750* (NY).

Licaria triandra (Sw.) Kosterm. Rec. Trav. Bot. Néerl. **34:** 588. 1937.

Laurus triandra Sw. Prodr. Veg. Ind. Occ. 65. 1788.

According to published accounts (e.g., Mez, 1889; Kostermans, 1937; Allen, 1945; Bernardi, 1962), this species has been regarded as restricted to the West Indies. Recently, however, H. Kurz has annotated many Central American collections as *Licaria triandra.* The plants at La Selva differ from other Central American collections in their smaller, more acuminate leaves and their narrower cupule margins. In these respects the La Selva plants actually resemble collections of this species from the West Indies more than they do those from Central America.

SPECIMENS EXAMINED. **Costa Rica.** HEREDIA: La Selva, *Hammel 11036* (DUKE), *Hammel & Trainer 10802-A* (DUKE), *Hartshorn 1105* (NY), *Holdridge 5249* (NY).

Ocotea floribunda (Sw.) Mez, Jahrb. Königl. Bot. Gart. Berlin **5:** 325. 1889.

Laurus floribunda Sw. Prodr. Veg. Ind. Occ. 65. 1788.
O. wachenheimii Benoist, Bull. Mus. Hist. Nat. (Paris) **30:** 510. 1924.
O. arenaensis Brooks, Kew Bull. **5:** 217. 1933.

The very fine reticulate venation of the leaves, the broad tepals, and the perfectly globose fruits borne on thick discoid cupules are unusual in *Ocotea* and make this species easily recognizable, even on herbarium sheets.

Although *Ocotea floribunda* is common in the West Indies, it is quite rare in Central America. Until recently, it was known from just three collections—two from Nicaragua (cited by Mez, 1889) and one from Costa Rica, *Tonduz 12876* (US!) (correctly identified by Pittier). Its rarity probably accounts for the fact that neither Standley (1937) nor Allen (1945) included this very distinctive species in their treatments.

The name *Ocotea wachenheimii* has been applied to South American specimens that appear to differ from the West Indian and Central American plants only in geographic origin. Although Bernardi (1962) recognized both species, his key does not actually distinguish them: the cupule of *O. floribunda* is said to be double margined; that of *O. wachenheimii,* completely flat and disk shaped. His descriptions, however, suggest that both species have flat, double-margined cupules. My own observations indicate that the cupules of fresh material from La Selva are indeed flat but not double margined; any suggestion of a double margin is an artifact of drying and not at all reminiscent of the condition in, for example, most *Licaria* species. From these observations and examination of herbarium specimens, evidence for maintaining *O. wachenheimii* distinct from *O. floribunda* is lacking.

Collections of this species from the West Indies do tend to have somewhat smaller leaves than those from Central and South America. However, it would be difficult, at best, to deduce the place of origin of any particular specimen from its morphology.

CENTRAL AMERICAN SPECIMENS EXAMINED. **Costa Rica.** GUANACASTE: Monte Verde, *Dryer 1599* (CR); Rincón de La Vieja, *Judziewicz 4300* (CR). HEREDIA: rd. to Río Sucio, *Hartshorn 1563* (CR); La Selva, *Hammel 8914* (DUKE), *9705* (DUKE), *11170* (DUKE), *Hartshorn 1351* (CR). CARTAGO: near Turrialba, *Holdridge 6739* (CR). PUNTARENAS: near Panama border, *Hartshorn 2165* (CR); Tucurrique, *Tonduz 12876* (US).

Ocotea leucoxylon (Sw.) De Lanessan, Pl. Utiles Colon. Franç. 156. 1886.

Laurus leucoxylon Sw. Prodr. Veg. Ind. Occ. 65. 1788.
Ocotea lenticellata Lundell, Wrightia **5:** 54. 1974. TYPE: Guatemala, *Gentle 9924* (holotype, LL!; isotype, DUKE!).
Ocotea lasseriana C. K. Allen, Mem. New York Bot. Gard. **10:** 90. 1964. TYPE: Venezuela, *Lasser 1868* (holotype, F!; isotype, US!).

The warty cupules, distant rather than clustered inflorescences, gray-green leaves, and unusual scaly lower-leaf surfaces make *Ocotea leucoxylon* very easy to recognize even on herbarium sheets. It is partly on the basis of these features that synonymy with *O. lenticellata* of Guatemala and *O. lasseriana* of Venezuela is here established. *Ocotea duotincta* Allen, also of Venezuela, seems very closely related, differing only in its brownish pubescence. *Ocotea leucoxylon* was formerly thought to occur only in the West Indies. The collections cited below from Guatemala and Belize were originally distributed as *Ocotea mayana* (Lundell) Lundell and probably are still labeled with that name in most her-

baria. Lundell later recognized this material as belonging to a species distinct from the type of *O. mayana* (*Gentle 3187* (holotype, MICH!)) and gave it the name *O. lenticellata.*

Howard (1981) traced the history of uncertain authorship for the combination *Ocotea leucoxylon* and concluded that Mez (1889) should be cited as the correct author. However, the rejection of *Ocotea leucoxylon* (Sw.) De Lanessan, an earlier combination for this same species, seems unjustified. De Lanessan (1886) did not cite Swartz, author of the basionym, but referred to Grisebach, who under *Oreodaphne leucoxylon* Griseb. (1864) did refer to the basionym and its author, Swartz. Clearly, De Lanessan was referring to this same species since the essential features of his description translate directly from Grisebach. Although this is a very indirect reference, it does lead back to *Laurus leucoxylon* Sw. Since the current ICBN Article 33.2 requires a complete and direct reference only for new combinations made after 1953, De Lanessan, whose work was published three years prior to that of Mez, should be given credit for the combination.

CENTRAL AMERICAN SPECIMENS EXAMINED. **Guatemala.** IZABAL: Puerto Mendez, *Contreras 9914* (LL), *9924* (LL), *10071* (DUKE), *10075* (LL, US), *10291* (DUKE); El Estor, *Contreras 11364* (LL, US), *11367* (DUKE); Cadenas, *Lundell & Contreras 19037* (LL). **Belize.** STANN CREEK: Humming Bird Hwy., *Gentle 8811* (LL). **Costa Rica.** HEREDIA: La Selva, *Grayum 2388* (DUKE), *Hammel 10912* (DUKE), *11058* (DUKE), *11928* (DUKE), *Hammel & Trainer 12957* (DUKE), *13123* (DUKE), *D. Smith 484* (DUKE). **Panama.** PANAMÁ: near Goofy Lake, Cerro Azul, 3 July, *Croat s.n.* (CR); Cerro Jefe, *D'Arcy & Sytsma 14748* (MO), *Sytsma & Antonio 2325* (MO); El Llano–Cartí road, *Mori et al. 4150* (MO).

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ALIEN SPECIES OF LEPIDIUM (CRUCIFERAE) IN HAWAII

REED C. ROLLINS[1]

The incidence of weeds in the flora of Hawaii is very high compared to that for other land areas of similar size. This is understandable, given the heavy destruction of the native flora at lower elevations, mainly for agricultural purposes, and the fact that Hawaii has long been a crossroads for international commerce and thus for weed seeds from all over the world. In a genus like *Lepidium,* which has many widespread weedy species, one would expect to find at least several species as components of the present-day Hawaiian flora. Oddly enough, only *L. virginicum* L. has been widely recognized as an alien (Hillebrand, 1888; Fagerlund, 1947; St. John, 1973).

Apparently the introduced species have not been closely studied in recent years, and there are indeed several more than one. These are all annuals, or winter annuals, in their native regions, but in Hawaii perennation sometimes occurs. They are markedly different from the species of *Lepidium* native to the Hawaiian Islands, which are shrubs or subshrubs and have been characterized as "bizarre" in contrast to the usual herbaceous taxa (Fosberg, 1972). Fosberg (1969) commented on one of these species, *L. bidentatum* Montin, and concluded that it occurs in its typical form on most of the coral islands of the southern, central, and eastern Pacific. *Lepidium bidentatum* appears to have provided the basic genetic stock from which the taxa of *Lepidium* indigenous to Hawaii have originated. These include *L. bidentatum* var. *o-waihense* (Cham. & Schldl.) Fosb., *L. bidentatum* var. *remyi* (Drake) Fosb., *L. arbuscula* Hillebrand, and *L. serra* H. Mann. *Lepidium orbiculare* H. St. John (1981) appears to be a variant of *L. serra.* If this assumption as to the origin of the native taxa is correct, the evolutionary development of *Lepidium* in Hawaii is consistent with that of other groups of Hawaiian biota where a single source provided the base for the diversity now present (see Carlquist, 1970). That there are no nonwoody species of *Lepidium* indigenous to Hawaii is also consistent with the fact that other genera of the Cruciferae are often woody on isolated islands while their relatives on continental land masses are herbaceous.

The following key has been developed to aid in the identification of these taxa. Under each species brief comments are given to emphasize distinctive characteristics and points of special interest.

[1]Gray Herbarium, 22 Divinity Avenue, Cambridge, Massachusetts 02138.

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KEY TO THE ALIEN SPECIES OF LEPIDIUM IN HAWAII

A. Cauline leaves fasciculate; plants completely glabrous; siliques broadly oblong, distinctly longer than broad, the apical notch shallow, with margins barely exceeding short style. ..... 1. *L. hyssopifolium.*

A. Cauline leaves single; plants with at least some trichomes on stems; siliques rotund to only slightly longer than broad, the apical notch prominent, with margins definitely exceeding style.

B. Cauline leaves simple, incised to entire; plants branched above or beginning near base.

C. Petals conspicuous, equaling or exceeding sepals; infructescences nearly same diameter almost to apex; siliques 2.5 mm or more long. . . 2. *L. virginicum.*

C. Petals absent or minute; infructescences narrowing toward apex; siliques 2 mm or less long. ..... 3. *L. densiflorum.*

B. Cauline leaves pinnately lobed, lobes entire to sparsely dentate; plants branched beginning near base.

D. Plants leafy up to infructescences, usually more than 2 dm tall; leaves often densely hirsute with large trichomes, each segment tapering to sharp, apiculate point; infructescences markedly narrowing toward apex. ..... 4. *L. bonariense.*

D. Plants with few leaves, usually less than 2 dm tall; leaves sparsely hirsute with small trichomes to glabrous, the segments oblong, obtuse or nearly so; infructescences narrowing only slightly toward apex. ..... 5. *L. oblongum.*

1. **Lepidium hyssopifolium** Desv. J. Bot. Agric. **3:** 17. 1814.

Outstanding features of *Lepidium hyssopifolium* are the mostly entire, linear, fasciculate cauline leaves, the small, broadly oblong siliques with a shallow sinus at the apex, the nearly sessile stigmas, the narrow, elongated infructescences, and the nearly glabrous plants. The Hawaiian specimen is completely glabrous. The branches tend to be strongly ascending, and the plants are usually taller than 4 dm.

Lepidium hyssopifolium was described from Australia, where it has become a widespread weed. There seems to be some question as to its provenance. Carolin and Hewson (1981) suggested that the species may have been introduced from South Africa, but Hewson (1981) listed it as native. I have seen no evidence that *L. hyssopifolium* is an alien in Australia, although I have not researched the point thoroughly. On the other hand, Burbidge and Gray (1970, p. 186) described it as "a native species widespread in higher rainfall areas of temperate Australia." According to Thellung (1906), the type came from Hawkesburg, New South Wales, and was collected by Ferdinand Bauer. It is doubtful whether the glabrous phase, named *L. pseudo-hyssopifolium* by Hewson (1981), is a distinct taxon. Many species of *Lepidium* have both pubescent and glabrous phases, often growing together.

The Hawaiian record is based on a single collection: Ahumoa, by abandoned radio facility at 7040 ft elev., 21 May 1975, *Herbst & Spence 53211* (BISH). Since this collection is very similar to those from Australia, it is probable that *L. hyssopifolium* was introduced from there to Hawaii.

2. **Lepidium virginicum** L. Sp. Pl. 645. 1753.

Among the annual species of *Lepidium* presently known in Hawaii, *L. virginicum* is the only one with conspicuous petals that equal or exceed the sepals in length. The plants are usually single stemmed and branched above the middle. It is only when the plant has been trampled or the main stem has been altered at an early stage of growth that branching occurs at lower levels. Compared to the other weedy *Lepidium* species of Hawaii, *L. virginicum* has larger, more rotund siliques. It is by far the commonest of the group.

3. **Lepidium densiflorum** Schrader, Index Sem. Horti Acad. Göttingen. 4. 1832.

In areas where both *Lepidium densiflorum* and *L. virginicum* occur as weeds, the two species are frequently confused. They can be readily distinguished because *Lepidium densiflorum* is apetalous (or if petals are present, they are minute), whereas *L. virginicum* has conspicuous petals that usually exceed the sepals in length. The flowering and fruiting racemes are very dense, as implied by the name, in *L. densiflorum,* and the fruiting racemes are narrow, further narrowing toward the apex; in *L. virginicum* the racemes are less dense, and they maintain the same diameter nearly to the top. In addition, the siliques of *L. densiflorum* are much smaller than those of *L. virginicum.*

4. **Lepidium bonariense** L. Sp. Pl. 645. 1753.

In its native South America, *Lepidium bonariense* L. is a widespread weed, and there is considerable variation in the abundance of trichomes on the leaves and stems. Specimens with the densest trichome covering appear to be centered in Brazil, while several from Argentina, determined by Hitchcock (1945b) as *L. bonariense,* are nearly glabrous except for the upper stems and pedicels. The one specimen we have seen from Hawaii (roadside weed, along Saddle Road on Waimea side of Pohakuloa State Park, 20 May 1975, *Herbst 5336* (BISH)), is densely pubescent, matching specimens from Brazil in this respect. However, there is a range of variation in the density of trichomes among material of *L. bonariense* from Australia, where the species is obviously alien. This suggests that such variation is usual in the species.

Features of *Lepidium bonariense* important for identification include the leafiness up to the infructescences, the relatively erect branches that tend to overtop the main axis, the minute (or absent) petals, the coarse simple trichomes usually present on both surfaces of the leaves and on the lower stems, and the pinnately lobed cauline leaves. The plants are characteristically single stemmed, but the branching may begin fairly low on the main stem axis.

Outside of South America, *Lepidium bonariense* has been widely recognized as an alien weed.

5. **Lepidium oblongum** Small, Fl. S.E. U. S. 468, 1331. 1903.

This is a low-growing species, seldom to 2 dm tall, with branches beginning at or near the base. In the Hawaiian material the fruit has a characteristic

U-shaped sinus and the margins of the siliques are fringed with minute trichomes. The pedicels are usually spreading, somewhat flattened, and covered with trichomes on their adaxial surfaces. The cauline leaves are few and deeply pinnately lobed. Most fully mature plants have lost the basal leaves. Both glabrous- and fringed-fruited plants occur in the southwestern continental United States and Mexico. The fringed condition is more prevalent westward from Arizona to California and southward through most of Mexico than it is in Arkansas, Oklahoma, and Texas.

One or two features of the Hawaiian material point to Mexico as a possible source for this introduction. One, stressed by Hitchcock (1945a), is late shedding of the sepals. In most plants of the species, they are shed very early: usually only two to four fully open flowers near the tip of the inflorescence will have retained them. In the Hawaiian specimens the sepals are retained in five to eight flowers of the upper inflorescence, a tendency also shown in several Mexican specimens. In addition, fruits of the Mexican specimens are more consistently fringed with trichomes than are those from elsewhere; since the Hawaiian specimens all show this feature, it rates as minor evidence in favor of a Mexican origin for the Hawaiian alien.

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60	1979	49	74	71	46	6.25	4.35
61	1980	101	91	119	314	6.25	4.35
62	1981	165	118	112	110	6.25	4.35
63	1982	69	73	116	92	6.25	4.35

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THE GENERA OF LOGANIACEAE IN THE SOUTHEASTERN UNITED STATES[1]

GEORGE K. ROGERS[2]

LOGANIACEAE C. F. P. Martius, Nov. Gen. Sp. Pl. Brasil. **2:** 133. 1827, "Loganieae," nom. cons.

(LOGANIA FAMILY)

Shrubs [trees] or vines, rarely herbs. Trichomes unicellular, uniseriate, or with a variable, multicellular, broadened head (mostly confined to the Buddlejeae), or candelabrum shaped (only Buddlejeae). Leaf bases, stipules, bracts,

[1]Prepared for the Generic Flora of the Southeastern United States, a long-term project made possible by grants from the National Science Foundation and at this writing supported by BSR-8111520 (Carroll E. Wood, Jr., principal investigator), under which this account was prepared, and BSR-8303100 (Norton G. Miller, principal investigator). This treatment, the 110th in the series, follows the format established in the first paper (Jour. Arnold Arb. **39:** 296–346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets [ ]. References that I have not verified are marked with an asterisk.

Particular gratitude is extended to V. Bates, I. W. Carpenter, S. Y. Hu, P. W. Leenhouts, A. J. M. Leeuwenberg, J. L. Reveal, T. J. Rosatti, and V. Sosa for variously sharing results of their own research, sending literature, providing distributional data, and answering questions. Eliane M. Norman generously set aside a portion of a trip to the Harvard Herbaria to discuss her work on *Buddleja,* reviewed the manuscript, and supplied a great deal of information; her contributions have substantially improved the paper.

Dorothy H. Marsh drew the illustrations in May, 1957, under the supervision of R. B. Channell and C. E. Wood, Jr. The figures are based on specimens in the herbaria of the Arnold Arboretum and Gray Herbarium and on spirit-preserved materials collected by R. B. Channell and H. F. L. Rock. Donna Rogers, my wife, is thanked for translating literature from French. Reviews of the manuscript by C. E. Wood, Jr., and N. G. Miller yielded improvements, as did E. B. Schmidt's and S. A. Spongberg's editorial efforts. Barbara Nimblett moved the project along quickly by performing much of the typing.

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and calyces often with colleters adaxially. Leaves usually opposite or infrequently whorled or pseudowhorled [or rarely alternate], simple, entire or toothed [to infrequently lobed], penninerved or with ascending, arcuate lateral nerves, or vasculature other than the midrib inconspicuous in reduced leaves. Stipules diverse, interpetiolar (then leafy, membranaceous, or reduced to a ridge or flange) or rarely represented by a pair of lobes flanking each petiole. Inflorescences terminal (then sometimes in forks between branches) or axillary, fundamentally cymose but otherwise variable, sometimes dichasial, cincinnous (then often spicate), fasciculate, thyrsiform, scorpioid, or paniculiform, sometimes tightly congested, occasionally with solitary flowers; showy bracts lacking. Flowers mostly actinomorphic or somewhat zygomorphic, perfect or infrequently imperfect, tetramerous or pentamerous. Calyx lobes separate or coalescent, often unequal. Corolla tubular, cylindrical to funnelform or urceolate, with variously oriented imbricate, valvate [or contorted] lobes, the tube often occluded by hairs. Stamens typically alternating with same number of corolla lobes [or reduced in number], epipetalous, usually uniform; anthers introrse, dehiscing longitudinally; pollen grains usually colporate (to colpate in *Spigelia*). Ovary superior to partly inferior, usually bilocular (tetralocular in *Buddleja madagascariensis*) [or rarely unilocular or with 3–5 partial or complete locules], containing [1 to] many anatropous, hemianatropous, or reportedly amphitropous ovules in each locule on axile, frequently peltate [or rarely parietal or basal] placentae; stigmas unlobed, 2-lobed, or 4-lobed. Fruits usually capsules with septicidal dehiscence predominant but also with varying degrees of loculicidal dehiscence, thus separating partly or completely into 2 (a pair of apical horns in some genera) or 4 segments [or infrequently loculicidal only], in some berries [or drupes]. Seeds usually numerous and small, winged or not, the embryo straight; endosperm initially nuclear or cellular [or intermediate], sometimes ruminate, surrounding the embryo; embryo sac (megagametophyte) of the Polygonum type. (Including Buddlejaceae Wilhelm, Samenpfl. 90. 1910, "Buddleiaceae," nom. cons.; Spigeliaceae Martius, Nov. Gen. Sp. Pl. Brasil. **2**: 132. 1827.) TYPE GENUS: *Logania* R. Brown, nom. cons.

As recently defined by Leeuwenberg & Leenhouts (to embrace the Buddlejaceae), a family of 29 genera and about 470 species in ten tribes distributed pantropically and subtropically with limited extensions into the temperate zones. The two largest genera, *Strychnos* L. and *Buddleja* L., are pantropical and contain between 90 and 200 species each. Seven genera grow free of cultivation in the continental United States. *Emorya suaveolens* Torrey, the sole species of its genus, is endemic to northern Mexico and southern Texas. The cultivated *Strychnos spinosa* Lam. escapes infrequently to disturbed places in Florida. As elaborated later, at least one species of *Buddleja* is naturalized in the southeastern United States, and species of *Mitreola* L. (*Cynoctonum* J. F. Gmelin), *Polypremum* L., *Spigelia* L., and *Gelsemium* Juss. are indigenous in the range of the Generic Flora.

The comprehensive treatment in the second edition of *Die Natürlichen Pflanzenfamilien* (1980) contains a taxonomic revision at the generic level (Leeuwenberg & Leenhouts) and stands as the principal modern work on the Loganiaceae. See Klett and Solereder (1892) for earlier revisions.

Broadly interpreted, the family is characterized, with exceptions, by opposite leaves with interpetiolar stipules (or sheaths, flanges, or ledges), fundamentally cymose inflorescences, actinomorphic (or weakly zygomorphic), tetramerous or pentamerous flowers, epipetalous stamens alternating with the lobes of the tubular corolla, and superior (or in some partly inferior), generally bilocular ovaries most often enclosing axile (sometimes peltate) placentae bearing numerous ovules. The seeds contain straight embryos. Most genera, other than *Buddleja,* its allies, and some others, have internal phloem and vestured pits on the vessel elements.

The subdivision, delimitation, and position of the Loganiaceae are longstanding problems. The family has been an artificial "catchall" for difficult-to-place genera. Moreover, it is relatively poor in obvious specialized characters and thereby resembles the ancestral stock from which related families arose. The Loganiaceae also show multiple links between their heterogeneous subunits and other families. Extreme taxonomic views have been to splinter the Loganiaceae into several smaller families (e.g., see Hutchinson) or to apportion its major components among related families (e.g., see Bureau).

Modern authors generally place the Loganiaceae in the inconsistently circumscribed order Gentianales (Contortae), with the Apocynaceae, Gentianaceae, and Rubiaceae receiving most attention as probable close relatives. The tribe Buddlejeae spans an ordinal boundary in that it shows similarities to the Scrophulariales (Tubiflorae).

The Loganiaceae *sensu stricto* and the Rubiaceae share several characters—interpetiolar stipules, colleters, wood sometimes accumulating aluminum and usually with vestured pits, pollen with similar wall stratification (Cronquist), and nuclear endosperm. The two families are further bound together, along with the Apocynaceae, by their tryptophan-tryptamine indole alkaloids (see Kisakürek *et al.*). With exceptions, the Rubiaceae differ from the Loganiaceae *sensu stricto* in their inferior ovaries and lack of internal phloem. (See discussion of the tribe Spigelieae below for one narrow gap between the Loganiaceae and the Rubiaceae.)

In their study of tryptophan-tryptamine indole alkaloids, Kisakürek and colleagues found that the Loganiaceae overlap even more with the Apocynaceae than with the Rubiaceae, and that they appear to be less specialized than either of these two families. The Apocynaceae and Loganiaceae both have internal phloem, vestured pits, nuclear endosperm, and colleters. Differences are that the Apocynaceae have a latex system (but note that the loganiaceous *Fagraea* Thunb. produces latex in fruits), mostly lack stipules, and tend to have both androecial and gynoecial specializations.

Similarities between the Gentianaceae and the Loganiaceae include internal phloem, colleters, xanthones, usually nuclear endosperm, and wood that sometimes accumulates aluminum (Cronquist; Bisset, 1980a). There are close morphological similarities. The Gentianaceae differ in lacking stipules (although interpetiolar flanges occur) and, with exceptions in both families, in having unilocular ovaries with parietal placentae.

Buddleja belongs to a collection of about seven genera of uncertain placement. Authors who give this group membership in the order Gentianales either treat

it as a family (e.g., Thorne) or assign it an infrafamilial rank in the Loganiaceae. Leeuwenberg & Leenhouts treated it as tribe Buddlejeae in the Loganiaceae, the rank and position adopted tentatively in the present paper. When placed in the order Scrophulariales (Tubiflorae), the Buddlejeae have been included in the Scrophulariaceae by some botanists, but most who advocate this ordinal placement (e.g., Cronquist, Melchior, Takhtajan) accept the separate family Buddlejaceae.

Taxonomic alignment of the Buddlejeae with the Loganiaceae rests largely upon transitional genera and a few morphological characters, in particular presence of stipules and actinomorphic or weakly zygomorphic corollas. On the other hand, most genera of the Buddlejeae stand apart in their lack of colleters, internal phloem, and vestured pitting (also absent in *Gelsemium* and a small number of other nonbuddlejaceous genera; see Mennega). They further stand apart in having pericyclic (vs. superficial) cork (*Peltanthera* Bentham, nom cons., and probably *Sanango* Bunting & Duke are exceptions in the Buddlejeae), endothelium in the ovule, cellular (vs. generally nuclear) endosperm, chromosome numbers based mostly on 19, complex trichomes with laterally adjacent cells making up broadened heads or tiers (vs. trichomes usually unicellular or uniseriate), an inconsistent tendency toward serrate leaves, and frequently tetramerous (vs. pentamerous) flowers having imbricate (vs. usually contorted or valvate) corolla lobes. (*Peltanthera* and *Sanango* are pentamerous exceptions in the Buddlejeae, and *Peltanthera* and *Buddleja* sometimes have valvate corolla lobes. Imbricate lobes appear in the Spigelieae in *Mitreola*.)

Intermediate genera complicate severing the Buddlejeae from the rest of the Loganiaceae. *Mitrasacme* Labill., which is usually placed in the Spigelieae, approaches the Buddlejeae in having intermediate endosperm and, reportedly, pericyclic cork in the root (Morelle). (Records of glandular trichomes in *Mitrasacme* are of dubious accuracy.) The somewhat similar and likewise intermediate genus *Polypremum* is discussed below.

Peltanthera and *Sanango,* especially, seem to approach the tribe Antonieae Endl. (Leenhouts, 1963). Leeuwenberg (1975) perceived similarities between *Nuxia* Lam., other genera of the Buddlejeae, and the tribe Antonieae in the capsule, endosperm, and embryo. Klett and Bunting & Duke stressed that *Logania* resembles the Buddlejeae.

Developmental evidence led Hasselberg (also see Weberling) to challenge the presumed homology between stipules in the Buddlejeae and other Loganiaceae; more work, however, is needed.

Affinity of the Buddlejeae with the Scrophulariaceae and other Scrophulariales is an old concept that is still sustained largely by embryological and chemical characters. Embryologically, the Buddlejeae agree far better with the Scrophulariales than with the other Loganiaceae (see Wagenitz, 1959; Dop; Davis); still, cellular endosperm and endothelia are widespread among flowering plants and sampling is spotty. Palynology has been invoked to support a scrophularian alignment (see Punt & Leenhouts), but after broadened sampling Punt (1980) concluded that palynology failed to support a relationship of the Buddlejeae with other tribes of the Loganiaceae.

In producing aucubins and related iridoids instead of seco-iridoids, *Buddleja* resembles the Scrophulariaceae and allies while diverging from several genera of the Loganiaceae and other Gentianales. Flavone 6-hydroxyluteolin and other flavonoids point *Buddleja* toward a scrophularian position. In a paper in which they documented this, Harborne & Williams used the similar compound scutellarein to tie the Plantaginaceae to the Tubiflorae (Scrophulariales) before Marin and colleagues (under *Buddleja*) isolated a glucoside of scutellarein from *B. globosa* Hope. Harborne (p. 287) mentioned crocein as "yet another [flavonoid] link between *Buddleja* and the Scrophulariaceae" and listed orobanchin and similar substances in *Buddleja, Catalpa* (Bignoniaceae), *Verbascum* (Scrophulariaceae), *Orobanche* (Orobanchaceae), and *Syringa* (Oleaceae). Weaknesses in the chemical evidence are that aucubins and similar compounds, as well as 6-hydroxylated flavones, including 6-hydroxyluteolin and scutellarein, have been detected in disparate families such as the Eucommiaceae, Rosaceae, Rubiaceae, and Compositae quite removed from the Scrophulariaceae. (For further discussion of the chemical data, see Daniel & Sabnis; Bisset, 1980a; and Jensen *et al.*)

Taxonomically selective pests add further links between *Buddleja* and the Scrophulariaceae. A leaf-mining fly and two species of weevils thought to attack only the latter transfer to *Buddleja,* and a species of the fungal genus *Peronospora,* otherwise restricted to hosts in the Scrophulariaceae, has been found on *B. globosa.* (The fungus on the *Buddleja* has been treated as a distinct species, however.) (See Hering; Mohrbutter; Wagenitz, 1959; and Williams, under *Buddleja,* for more on this line of evidence.)

According to Cronquist (p. 947), Piechura showed "strong serological affinities between the Buddlejeae and several tested families of Scrophulariales." The irregular pentamerous flowers of *Sanango* (*Gomara*) with four (nondidymous) fertile stamens and a sterile staminode further attracted Cronquist's attention as a similarity between the Buddlejeae and the Scrophulariales (also pointed out by Bunting & Duke).

For discussion of the possible relationship between the Buddlejeae and the Scrophulariales, see Hakki, Hasselberg, Hunzicker & Di Fulvio, Leenhouts (1963), Solereder (1892), Tiagi & Kshetrapal, and Wagenitz (1959); under *Buddleja* see Souèges.

Altogether, the Buddlejeae seem bound to the other Loganiaceae by intermediate genera and very weakly by the widespread as well as questionably homologous characteristics of stipules and actinomorphy, while they differ in numerous but overlapping features. *Buddleja,* and to an uncertain extent the other Buddlejeae, resemble the Scrophulariales in a set of widespread embryological characteristics and in chemical traits, all of which are too generalized to be trusted without reservation. Sampling remains disconcertingly skimpy for the difficultly evaluated characters.

Students of the Loganiaceae gather *Spigelia, Mitreola, Mitrasacme,* and sometimes *Polypremum* together either as an infrafamilial taxon of varying rank or as a separate family. Leeuwenberg & Leenhouts recognized this assemblage, including *Polypremum,* as the tribe Spigelieae. With exceptions the following characters help to unite the tribe: herbaceous growth; pseudodichoto-

mous-dichasial branching; arcuate foliar nerves; cincinnous units in the inflorescences; thin corollas; partly inferior ovaries (superior in *Spigelia*); peltate, rounded seeds on peltate placentae; and apically bilobed capsules of questionable homology. Palynological evidence, however, is divisive, except that the pollen tends to be oblate (Punt, 1980). Punt (1980) found each of four main pollen types within the Spigelieae to agree best with genera outside the tribe.

The capsular fruits offer the most convenient distinctions between genera of the Spigelieae. Those of *Spigelia* are markedly bilobed apically with the uniquely articulated style inserted in the cleft between the lobes. The capsules dehisce to leave behind cuplike or boatlike bases on the plant (see FIGURE 1j). As the capsule matures in *Mitreola* and *Mitrasacme,* the upper portion of the two carpels separates into a pair of horns that open longitudinally face to face. Either separation of the horns splits the style lengthwise, or the style remains partly intact apically and bridges the horns; occasionally the style remains completely intact on one horn (see FIGURE 2e). Many undehisced capsules of *Polypremum* slightly resemble those of *Spigelia* in being indented apically; upon dehiscence they appear a little like those of *Mitreola* and *Mitrasacme,* parting into a pair of apical lobes, each of which opens along adaxial lines. In *Polypremum,* however, both the abaxial and the adaxial walls tend to open, the apical lobes are not as distinctly or as precociously developed as the horns in the other two genera, and the style remains whole.

Flowers in the Spigelieae are pentamerous (*Mitreola, Spigelia*) or tetramerous (*Polypremum, Mitrasacme*) and have imbricate (*Polypremum* and sometimes *Mitreola*) or more or less valvate aestivation (*Spigelia, Mitrasacme,* and sometimes *Mitreola*). *Mitrasacme* (with exceptions), *Mitreola,* and *Polypremum* have partly inferior ovaries, as opposed to superior ovaries in *Spigelia.* The flowers are borne along cincinnous branches in *Mitreola,* most species of *Spigelia* (in others flowers are few in monochasia or in small, essentially monochasial pseudoumbellate clusters), and infrequently in *Polypremum* (where they are also arranged singly between dichasial branches or otherwise). Flowers of *Mitrasacme* are either solitary or in pseudoumbellate cymes.

Vegetative traits are least useful for distinguishing genera of the Spigelieae. Leaves often in rosettes help to set *Mitrasacme* apart from *Mitreola.* Extensive pseudodichotomous-dichasial branching, sprawling or broomlike habit, various scabrous-serrulate organs, and nearly linear leaves characterize, but are not unique to, *Polypremum.*

Modern botanists agree that the placement of *Polypremum* in the Rubiaceae is incorrect (see Moore under *Polypremum*; see also Punt & Leenhouts), but its position in the Spigelieae is not free from controversy. Assignment to the Buddlejeae is plausible.

As justification for numbering *Polypremum* among the Spigelieae, Leenhouts (1962) listed its herbaceous habit, membranaceous interpetiolar stipular sheaths (also found in Buddlejeae), partly inferior ovaries, and nearly basal peltate placentae (vs. placentae usually axile in Buddlejeae, except *Peltanthera,* which in published illustrations appears to have more or less peltate placentae). Additional features to be found with varying degrees of prevalence in both *Polypremum* and the Spigelieae are reduced leaves (reappearing in the Buddlejeae),

pseudodichotomous-dichasial branching, flowers in cincinni, seeds broader than long and attached peltately (vs. usually elongate and attached at the ends in the Buddlejeae, but note that seeds much like those of *Polypremum* are found in *Gomphostigma* and rarely in *Buddleja*), palisade parenchyma in the stem (see Morelle for this in *Spigelia*), and superficial initiation of cork. (For a report of superficial cork in *Polypremum,* see Metcalfe & Chalk.) Cork is pericyclic in members of the Buddlejeae, except *Peltanthera.* Morelle reported an exceptional instance of cork forming deep in the cortex in *Spigelia* and in the root in *Mitrasacme.* Vegetatively, *Polypremum* is especially reminiscent of *Mitrasacme,* some species of which, moreover, have tetramerous flowers much like those of *Polypremum.* Capsules not much different from those of *Polypremum* occur in *Mitreola.* (The vegetative habit, flower, and capsules of *Polypremum* could, nevertheless, be readily accommodated in the Buddlejeae.) Punt & Leenhouts interpreted palynological evidence to indicate *Polypremum* as closer to the Spigelieae. (Punt, 1980, later concluded that *Polypremum* resembles *Mitrasacme* palynologically but is even more like *Strychnos.*)

Polypremum resembles genera of the Buddlejeae more than genera of the Spigelieae in having trichomes with broadened multicellular heads. Yet there exist a few indications of hairs with multicellular heads in the Spigelieae: the "stellate hairs" of some species of *Spigelia* differ in structure from other types of trichomes under consideration here, although Hurley's mention of multicellular glandular hairs in this genus warrants further checking. Reports of complex hairs in *Mitrasacme* are probably wrong. Further points of resemblance between *Polypremum* and the Buddlejeae are the integumentary tapetum (endothelium) in the ovule (but this uniquely becoming the principal hardened layer in the seed coat in *Polypremum*), cellular endosperm (vs. endosperm nuclear or intermediate in the Spigelieae), possible possession of the flavone scutellarein (Harborne & Williams; Marin *et al.,* under *Buddleja*), and chromosomal size and morphology (Moore, 1947). *Polypremum* and the Buddlejeae depart from the Spigelieae in lacking colleters, internal phloem, and vestured pitting. For the last two characters at least one examination is either recorded in the literature or has been made in the course of preparing this paper for all genera of Spigelieae. In the Buddlejeae *Buddleja, Sanango,* and *Peltanthera* have been checked for internal phloem; the nature of pitting in vessel elements has been verified for all except *Sanango.* (I used a scanning electron microscope to examine pitting on vessel elements from every genus of the Spigelieae and from *Peltanthera, Buddleja,* and *Emorya* in the Buddlejeae.) The generalized or negative nature of most of the characters cited in connection with the placement of *Polypremum* leaves few obvious specializations shared with either set of potentially closest relatives.

If members of the Spigelieae belong together, they may be most closely related to members of the tribe Loganieae, as hinted by limited resemblances in cytology (Gadella), wood anatomy (Mennega), and morphology (Leeuwenberg & Leenhouts).

In view of the suspected proximity of the Loganiaceae and the Rubiaceae, it is of interest to note that members of the Spigelieae and the rubiaceous tribe Hedyotideae show dichasial branching, interpetiolar stipules, colleters, arcuate

foliar nerves, similarities in wood anatomy (Mennega), partly inferior ovaries containing numerous, often peltate ovules on stalked placentae, resemblances in floral vasculature (Tiagi & Kshetrapal), small, sculptured seeds, and markedly two-parted capsules (these sometimes bilobed apically and dehiscing both loculicidally and septicidally). *Mitrasacmopsis* Jovet is an intermediate genus generally placed in the Rubiaceae, although it resembles *Mitrasacme*.

The Spigelieae differ from the Hedyotideae palynologically, as well as in having internal phloem (lacking in *Polypremum*) and in (usually?) lacking raphides (but see Morelle, and Holm (1907, under *Spigelia*)).

Various members of the Loganiaceae are used as ornamentals and as sources of drugs, poisons, and medicines. Among those cultivated in warm-temperate and tropical gardens are *Strychnos spinosa* (Natal orange), species of *Spigelia, Gelsemium sempervirens, Nuxia floribunda* Bentham, *Desfontainia spinosa* Ruiz & Pavón, species of *Fagraea, Geniostoma ligustrifolium* A. Cunn., and over 25 species, cultivars, and hybrids of *Buddleja*. A few species of *Buddleja* are hardy in cool-temperate gardens. Foremost among the genera that yield bioactive substances is *Strychnos,* a genus well known for its wealth of alkaloids, in addition to iridoids, saponins, and no doubt other compounds with toxic or pharmacological potency. Species of *Strychnos* yield fish poisons, folk remedies, and drugs. Derivatives are ingredients in curares, from which indirectly came the surgical muscle-relaxant alcuronium. Other alkaloidal drugs from *Strychnos* are brucine and strychnine (the latter most familiar as a rat poison). *Strychnos potatorum* L. f. clears turbid water. (For a review of uses for Loganiaceae, see Bisset, 1980b.)

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Buddleja, and extralimital genera; 13 structural types of trichomes characterized and illustrated. Using literature (including LEEUWENBERG's revision of *Mostuea* and MORELLE's detailed report) and limited herbarium specimens, I have been unable to confirm peltate trichomes in *Mostuea.*]

———. Floral sclereids in some Loganiaceae. Proc. Indian Acad. Sci. B. **81:** 174–180. 1975a. [Thirty-three taxa examined, sclereids in flowers found in four extralimital genera.]

———. Patterns of nodal anatomy in Loganiaceae. Curr. Sci. Bangalore **44:** 99. 1975b. [Species of *Buddleja, Strychnos,* and *Gomphostigma*; includes limited data from literature; nodes multilacunar and unilacunar.]

BENTHAM, G. Scrophulariaceae. *In:* A. P. DE CANDOLLE, Prodr. **10:** 186–586. 1846. [Included *Buddleja* (in sections), *Polypremum,* and *Chilianthus,* 432–447.]

———. Notes on Loganiaceae. Jour. Linn. Soc. Bot. **1:** 52–114. 1857. [Includes comparison of *Gelsemium* "*nitidum*" with *G. elegans,* synonymy in *Spigelia,* position of *Polypremum,* tribal subdivision of family, "Species Prodromo Candolleano addendae vel emendandae" (90), and commentary on BUREAU's treatment of the Loganiaceae (112–114). The following metaphor (p. 54) helps to illustrate Bentham's views on the position of the Loganiaceae: ". . .the Rubiaceae, Apocyneae, Gentianeae, and Scrophularineae would be typified by large and dense woods rather widely separated from each other, but the intervening space would be dotted over with solitary trees or small clusters representing our Loganiaceae."]

——— & J. D. HOOKER. Loganiaceae. Gen. Pl. **2:** 786–799. 1876. [Three tribes, one with five subtribes.]

BISSET, N. G. 8. Phytochemistry [of Loganiaceae]. Nat. Pflanzenfam. ed. 2. **28bI:** 211–237. 1980a. [*Gelsemium* with alkaloids, scopoletin, emodin monomethyl ether, and other compounds; *Buddleja* reputedly forming alkaloids but poorly known in this regard, possibly with saponins, with aucubin, catalpol, O-methylcatalpol, probable aucubin and catalpol esters, caffeic and ferulic acids, orobanchin (buddleoside), kaempferol, quercetin, linarin, 6- and 8-hydroxy-luteolin, acacetin, luteolin, and buddledin sesquiterpenes (see YOSHIDA *et al.* under *Buddleja*).]

———. 9. Useful plants [Loganiaceae]. *Ibid.* 238–244. 1980b. [A survey of utilization of the Loganiaceae by humans, some applications related to modern chemistry and medicine; folk remedies and poisons predominate.]

———, T. W. J. GADELLA, A. J. M. LEEUWENBERG, A. M. W. MENNEGA, & W. PUNT. 1. General discussion of relationships between taxa inside and with taxa outside the family [Loganiaceae]. Nat. Pflanzenfam. ed. 2. **28bI:** 3–7. 1980.

BLACKWELL, W. H., JR. Flora of Panama. VIII. Loganiaceae. Ann. Missouri Bot. Gard. **54:** 393–413. 1967 [1968]. [Includes *Spigelia, Cynoctonum* (= *Mitreola*), *Buddleja,* and *Polypremum* (expected in Panama).]

BREMEKAMP, C. E. B. The African species of *Oldenlandia* L. sensu Hiern et K. Schumann. Verh. Nederl. Akad. Wet. Afd. Natuurk. 2. **48**(2): 1–297. 1952. ["The delimitation and the subdivision of the Hedyotideae," 18–25.]

BUNTING, G. S., & J. A. DUKE. *Sanango*: New Amazonian genus of Loganiaceae. Ann. Missouri Bot. Gard. **48:** 269–274. *pl. 4.* 1961. [*Cf.* BARRINGER for generic name.]

BUREAU, L. E. De la famille des Loganiacées, et des plantes qu'elle fournit à la médecine. 150 pp., *1 pl.* Paris. 1856. [Classification of the Loganiaceae, 38; two "suborders" and seven tribes; *Gelsemium* in the Apocynaceae; *Mitreola, Mitrasacme,* and *Polypremum* in the Rubiaceae.]

CANDOLLE, A. P. DE, & A. DE CANDOLLE. Loganiaceae. *In:* A. P. DE CANDOLLE, Prodr. **9:** 1–37, 560, 561. 1845. [Four "suborders" and 11 tribes.]

CORRELL, D. S., & H. B. CORRELL. Flora of the Bahama Archipelago. 1692 pp. Vaduz, Liechtenstein. 1982. [*Mitreola petiolata, M. sessilifolia, Polypremum procumbens, Spigelia Anthelmia,* all illustrated, 1110–1117.]

——— & M. C. JOHNSTON. Manual of the vascular plants of Texas. xv + 1881 pp. +

map. Renner, Texas. 1970. [Includes *Gelsemium, Spigelia, Cynoctonum* (= *Mitreola*), *Polypremum, Buddleja,* and *Emorya,* 1200–1204.]

CRONQUIST, A. An integrated system of classification of flowering plants. xviii + 1262 pp. New York. 1981. [Loganiaceae, 865–867, in Gentianales; Buddlejaceae, 946–948, in Scrophulariales.]

DAHLGREN, R. General aspects of angiosperm evolution and macrosystematics. Nordic Jour. Bot. **3:** 119–149. 1983. [Loganiaceae, 138, 145, in Gentianales; Buddlejaceae, 145, in Scrophulariales; discusses circumscription of the Loganiaceae.]

DANIEL, M., & S. D. SABNIS. Chemotaxonomy of Loganiaceae. Curr. Sci. Bangalore **48:** 383–385. 1979. [*Strychnos* (two spp.), *Cynoctonum Mitreola* (*Mitreola petiolata*) and *Buddleja* (six spp.) screened for flavonoids, phenolic acids, and iridoids; alleged absence of alkaloids in Buddlejoideae contradicted by BISSET (1980a); specimens not vouchered; sample size small.]

DAVIS, G. L. Systematic embryology of the angiosperms. x + 528 pp. New York, London, and Sydney. 1966. [Loganiaceae, 16, 164; Buddlejaceae, 62, 63; *cf.* HAKKI.]

DON, G. A general system of gardening and botany. [A general history of dichlamydeous plants.] Vol. 4. viii + 908 pp. London. 1837–1838. [Spigeliaceae, 169–173.]

DOP, P. Remarques sur les Loganiacées. Bull. Soc. Bot. France **70:** 136–139. 1923. [Mostly a discussion of placement of *Buddleja* and allies; advocates alliance with Scrophulariales.]

DUNCAN, W. H., & J. T. KARTESZ. Vascular flora of Georgia. An annotated checklist. ix + 143 pp. + index. Athens, Georgia. 1981. [Includes *Gelsemium Rankinii, G. sempervirens, Spigelia marilandica, Mitreola petiolata* (as *Cynoctonum Mitreola*), *Mitreola sessilifolia* (as *C. sessilifolium* var. *sessilifolium* and var. *angustifolium*), *Polypremum procumbens, Buddleja Davidii,* and *B. Lindleyana,* 104.]

ECCLES, R. G. The natural order of Loganiaceae. Pharm. Record **8:** 41–44. 1888. [Concerned primarily with phytogeography and poisonous properties of *Strychnos.*]

ERDTMAN, G. Pollen morphology and plant taxonomy. (Corrected reprint of the 1952 edition with a new addendum.) *Frontisp.* + xiii + 553 pp. New York. 1971. [Loganiaceae, 246–249; includes illustrations of grains from *Buddleja, Gelsemium,* and *Spigelia.*]

GADELLA, T. W. J. 7. Cytology [of Loganiaceae.] Nat. Pflanzenfam. ed. 2. **28bI:** 202–210. 1980. [Also see ORNDUFF's chromosome counts (1970, under *Gelsemium*); includes synopsis of cytological literature on *Buddleja* and table of chromosome numbers with references for the Loganiaceae; ca. 20 percent of family studied cytologically; chromosomes fairly homogeneous in shape and usually small.]

GIBSON, D. N. Loganiaceae. Fl. Guatemala. Fieldiana Bot. **24**(8): 276–301. 1969. [Includes *Buddleja, Cynoctonum* (= *Mitreola*), *Gelsemium, Polypremum,* and *Spigelia.*]

GODFREY, R. K., & J. W. WOOTEN. Aquatic and wetland plants of southeastern United States. Dicotyledons. x + 933 pp. Athens, Georgia. 1981. [*Gelsemium, Spigelia, Polypremum, Mitreola,* 514–523; *M. petiolata, M. angustifolia,* and *M. sessilifolia* recognized and illustrated.]

GRAY, A. Synoptical flora of North America. Vol. II. Part I. vii + 402 pp. New York, London, and Leipzig. 1878. [Loganiaceae (in tribes), *Gelsemium, Spigelia, Mitreola, Polypremum, Buddleja, Emorya,* 106–110.]

GUÉDÈS, M. La ligule vraie chez les Loganiacées et les Rubiacées. Compt. Rend. Acad. Sci. Paris, D. **274:** 2471–2474. 1972.

HAKKI, M. I. 6. Embryology [of Loganiaceae]. Nat. Pflanzenfam. ed. 2. **28bI:** 192–201. 1980.

HALLÉ, F. 3. Vegetative architecture [of Loganiaceae]. Nat. Pflanzenfam. ed. 2. **28bI:** 97–111. 1980.

HARBORNE, J. B. The evolution of flavonoid pigments in plants. Pp. 271–295 *in* T. SWAIN, ed., Comparative phytochemistry. London and New York. 1966. [Crocein and orobanchin seem to pull *Buddleja* toward Scrophulariales.]

——— & C. A. WILLIAMS. 6-hydroxyluteolin and scutellarein as phyletic markers in higher plants. Phytochemistry **10:** 367–378. 1971. [Includes distributions of both "markers"; both indicative of scrophularialian affinities; *Buddleja* (and *Chilianthus*) with 6- and 8-hydroxyluteolin, acacetin, luteolin, quercetin, and kaempferol; *Gelsemium sempervirens* with quercetin and kaempferol; *Polypremum procumbens* possibly with scutellarein.]

HASSELBERG, G. B. E. Zur Morphologie des vegetativen Sprosses der Loganiaceen. Symb. Bot. Upsal. **2**(3). [vii +] 170 pp. 1937. [Includes discussion of subdivision of family; stipular development in *Nicodemia* and *Chilianthus* agrees with *Buddleja*.]

HEGNAUER, R., & P. KOOIMAN. Die systematische Bedeutung von iridoiden Inhaltsstoffen im Rahmen von Wettstein's Tubiflorae. (English abstract.) Pl. Med. **33:** 1–33. 1978. [Buddlejaceae, 17; includes chemical evidence for admitting the Buddlejaceae into the Tubiflorae; mentions iridoid similarity between *Chilianthus* and *Nuxia; Buddleja* with aucubin, catalpol, 6-methylcatalpol, and presumed aucubin and catalpol esters.]

HERING, E. M. Biology of the leaf miners. iv + 420 pp. The Hague, Netherlands. 1951. [*Buddleja,* 173, 196; the fly *Dizygomyza verbasci* Bché. on Scrophulariaceae and *Buddleja*.]

HOSSEUS, C. C. Loganiáceas. Revista Centro Estud. Farm. **2**(5): 1–30, *pls.* [*1, 2*]. 1926. [Placement, subdivision, and delimitation of the Loganiaceae and affinities of *Buddleja* discussed; includes uses of and miscellaneous notes on several species.]

HUNZIKER, A. T., & E. DI FULVIO. Observaciones morfológicas sobre *Peltanthera* (Loganiaceae), con referencia a su posición sistemática. Bol. Acad. Nac. Ci. Córdoba **40:** 217–228. *pl. 1.* 1958. [Of interest in connection with relationships and subdivision of the Loganiaceae.]

HUTCHINSON, J. Loganiales. Fam. Fl. Pl. ed. 3. Pp. 459–468. 1973. [Potaliaceae, Loganiaceae, Buddlejaceae, Antoniaceae, Spigeliaceae, Strychnaceae, Oleaceae.]

JENSEN, S. R., B. J. NIELSEN, & R. DAHLGREN. Iridoid compounds, their occurrence and systematic importance in the angiosperms. Bot. Not. **128:** 148–180. 1975. [*Buddleja*(ceae), 165–167, 170. "*Buddleja* has been reported to contain Group I iridoids typical of Scrophulariales but not of Gentianales. However, iridoids of Group I are found in a large part of Rubiaceae and a few species of Apocynaceae, though none of the iridoids in these families are identical with those in Buddlejaceae" (p. 166).]

JOVET, P. Aux confins des Rubiacées et des Loganiacées. Not. Syst. Paris **10:** 39–53. 1941. [Includes detailed comparison of the rubiaceous *Anotis, Astiella,* and *Mitrasacmopsis* with *Mitreola*.]

KISAKÜREK, M. V., A. J. M. LEEUWENBERG, & M. HESSE. A chemotaxonomic investigation of the plant families of Apocynaceae, Loganiaceae, and Rubiaceae by their indole alkaloid content. Pp. 211–376 *in* S. W. PELLETIER, ed., Alkaloids: chemical and biological perspectives. Vol. 1. 1983. [Comparison of families for indole alkaloids, 259–261, 272, 275; "Analysis of the Tribes of the Loganiaceae," 271, 272; report covers ca. 407 species from 50 genera; in the Loganiaceae indole alkaloids found in *Gelsemium, Mostuea, Gardneria,* and (predominantly) *Strychnos.* The three families have in common (almost uniquely) tryptophan-tryptamine indole alkaloids bearing a C_9- or C_{10}-moiety derived from secologanin. Three subtypes of these alkaloids occur in all three families; the aspidospermatan and strychnan types are limited to the Apocynaceae and the Loganiaceae.]

KLETT, W. Umfang und Inhalt der Familie der Loganiaceen. Bot. Arch. **5:** 312–338. 1924. [Largely concerned with delimitation, subdivision, and relationships of the Loganiaceae; advocates retaining the Buddlejeae in the Loganiaceae (see especially 317, 318); includes thorough literature review of higher-level taxonomy of the Loganiaceae, key to genera, generic descriptions, infrafamilial classification, discussion of relationships of *Chilianthus* and *Nicodemia* with *Buddleja,* 331–333, and com-

ments on relationships of *Polypremum,* 329; report of glandular hairs in *Mitrasacme* dubious.]

KSHETRAPAL, S., & Y. D. TIAGI. A contribution to the vascular anatomy of the node in certain species of the Gentianales. Jour. Indian Bot. Soc. **60**(3&4): 433–439. 1982.*

LEENHOUTS, P. W. Loganiaceae. *In:* C. G. G. J. VAN STEENIS, ed., Fl. Males. I. **6:** 293–387. 1962 [1963]. [Includes *Buddleja* (with all three of our species), *Gelsemium, Spigelia Anthelmia,* and *Cynoctonum* (= *Mitreola*); discusses positions of *Polypremum* (placed in the Spigelieae) and *Buddleja* with allies (tribe of the Loganiaceae); *Nicodemia* a subgenus of *Buddleja*.]

———. Addenda, corrigenda et emendanda. Loganiaceae. *Ibid.* 953–960. 1972.

LEESER, O. Plants and alkaloids, using the Loganiaceae as examples. (English transl. by H. AGERTY, summary by D. GLADISH.) Jour. Am. Inst. Homeopathy **29:** 730–732. 1936. [*Gelsemium, Spigelia.*]

LEEUWENBERG, A. J. M. The Loganiaceae of Africa. II. A revision of *Mostuea* Didr. Meded. Landb. Wageningen **61**(4): 1–31. 1961. [Compared with *Gelsemium.*]

———. Notes on American Loganiaceae. V. Key to the genera represented in America. Acta Bot. Neerl. **20:** 539–542. 1971. [Includes list of tribes.]

———. Loganiacées. Fl. Cameroun **12:** 1–153. 1972. [Includes *Mitreola, Spigelia Anthelmia.*]

———. The Loganiaceae of Africa XIV. A revision of *Nuxia* Lam. Meded. Landb. Wageningen **75**(8): 1–80. 1975. [This genus shows affinities in capsule, endosperm, and embryo to the loganiaceous tribe Antonieae and is close to *Buddleja* and relatives.]

———. Loganiaceae. Fl. Zambesiaca **7:** 327–374. 1983. [Includes all species of *Buddleja* in our range and illustrations of *Gomphostigma, Mostuea,* and other genera.]

———. Loganiacées. *In:* J. F. LEROY, Fl. Madagascar Comores **167:** 1–107. 1984. [Includes *Mitreola* and *Buddleja.*]

——— & P. W. LEENHOUTS. 2. Taxonomy [of Loganiaceae]. Nat. Pflanzenfam. ed. 2. **28bI:** 8–96. 1980. [Includes taxonomic history, chart showing infrafamilial classification to generic level in six works (see also KLETT), distributional notes, uses, morphology, position, relationships within family, and taxonomic revision of tribes and genera (individual species not treated).]

LONG, R. W., & O. LAKELA. A flora of tropical Florida. xvii + 962 pp. Coral Gables. 1971. [*Gelsemium, Polypremum, Spigelia, Cynoctonum* (= *Mitreola*), *Buddleja,* 689–692.]

LOUNSBERRY, A. Southern wild flowers and trees. *Frontisp.* + xxxi + 570 pp. + *177 pls.* New York. 1901. [*Gelsemium, Spigelia,* 423–425, *pl. 140.*]

MACBRIDE, J. F. Loganiaceae. Fl. Peru. Publ. Field Mus. Bot. **13**(5): 239–269. 1959. [Includes *Buddleja, Spigelia,* and *Cynoctonum* (= *Mitreola*).]

MARTIN, A. C. The comparative internal morphology of seeds. Am. Midl. Nat. **36:** 513–660. 1946. [Loganiaceae, 589, 627.]

MELCHIOR, H. Buddlejaceae. *In:* H. MELCHIOR, A. Engler's Syllabus der Pflanzenfamilien. ed. 12. **2:** 447, 448. 1964. [In order Tubiflorae, suborder Solanineae; for Loganiaceae see WAGENITZ (1964).]

MENNEGA, A. M. W. 4. Anatomy of the secondary xylem [of Loganiaceae]. Nat. Pflanzenfam. ed. 2. **28bI:** 112–161. 1980.

METCALFE, C. R., & L. CHALK. Anatomy of the dicotyledons. Vol. 2. *Frontisp.* [+ i] + pp. 725–1500. London. 1950. [Loganiaceae, see especially 925–933; includes discussion of SOLEREDER's subfamilies.]

MILANO, V. A. Las plantas cultivadas en la Republica Argentina. Loganiáceas. Min. Agr. Ganadería. Vol. **9**(Fasc. 162): 1–16. 1951. [Includes *Buddleja* (with all three of our species) and *Gelsemium sempervirens.*]

MOHR, C. Plant life of Alabama. Alabama ed. *Frontisp.* + xii + 921 pp. + *13 pls.* Montgomery, Alabama. 1901. [*Gelsemium, Spigelia, Cynoctonum* (= *Mitreola*), *Polypremum,* 668, 669.]

MOHRBUTTER, C. Embryologische Studien an Loganiaceen. Planta **26:** 64–80. 1936. [*Fagraea, Strychnos.*]

MOORE, R. J. Cytotaxonomic studies in the Loganiaceae. I. Chromosome numbers and phylogeny in the Loganiaceae. Am. Jour. Bot. **34:** 527–538. 1947. [Includes illustrations of chromosomes in *Gelsemium sempervirens, Polypremum procumbens, Spigelia marilandica,* and all of our species of *Buddleja*; also includes distribution map for *Buddleja,* taxonomic history of the family, and discussion of familial relationships; chromosome numbers determined for 24 species in seven genera plus 17 variants of *B. Davidii.*]

MORELLE, E. Histologie comparée des Gelsémiées et Spigéliées. Univ. Paris École Supér. Pharm. Ann. 1903–1904. No. **4.** iii + 162 pp. 1904. [An overlooked work rich in anatomical and other data on *Gelsemium sempervirens, Spigelia marilandica, S. loganioides, S. texana, S. Anthelmia, Mitreola petiolata, M. sessilifolia,* and extralimital genera and species; generic anatomical descriptions provided.]

MORTON, J. F. Atlas of medicinal plants of Middle America. Bahamas to Yucatan. xxviii + 1420 pp. Springfield, Illinois. 1981. [*Buddleja americana, Spigelia Anthelmia,* 664, 665.]

NORTON, J. B. S., & R. G. BROWN. A catalog of the vascular plants of Maryland. Castanea **11:** 1–50. 1946. [Includes *Polypremum,* 33, but not *Spigelia.*]

PATEL, R. C., G. GEORGE, & J. A. INAMDAR. Structure and development of stomata in some Buddlejaceae. Feddes Repert. **92:** 527–534. 1981. [*Buddleja* and *Nicodemia,* mature stomata variable.]

PERKINS, K. D., & W. W. PAYNE. Guide to the poisonous and irritant plants of Florida. Univ. Florida Inst. Food Agr. Sci. Florida Coop. Ext. Serv. Circ. **441:** 1–91. 1980. [*Gelsemium,* 26; *Spigelia,* 49; *Strychnos,* 90; *S. spinosa* and possibly *S. nux-vomica* cultivated in Florida.]

PERRY, L. M. (with the assistance of J. METZGER). Medicinal plants of East and Southeast Asia: attributed properties and uses. ix + 620 pp. Cambridge, Massachusetts, and London. 1980. [Loganiaceae, 243–245; includes *Gelsemium* and *Buddleja*; *B. Lindleyana* poisonous.]

PROGEL, A. Loganiaceae. In C. F. P. MARTIUS, Fl. Brasil. **6**(1): 249–300. *pls. 67–82.* 1868. [Four tribes; includes *Spigelia* (with sections) and *Mitreola* (*pl. 82* partly of *M. petiolata*); *Buddleja* treated by J. A. SCHMIDT in **8**(1): 282–286. 1862.]

PUNT, W. Evolutionary trends in the Buddlejeae (Loganiaceae). *In:* Fourth Internat. Palynol. Conf. Proc. **1:** 285–290. 1978.*

———. Pollen morphology [of Loganiaceae]. Nat. Pflanzenfam. ed. 2. **28bI:** 162–191. 1980. [See HOC & BRAVO (under *Spigelia*) for more recent survey of some genera that disagrees substantially with PUNT.]

——— & P. W. LEENHOUTS. Pollen morphology and taxonomy in the Loganiaceae. Grana Palynol. **7:** 469–516. 1967. [Reprinted as Meded. Bot. Mus. Herb. Rijksuniv. Utrecht **295.** 1967; updated with revised taxonomic conclusions in PUNT (1980); includes photomicrographs of pollen from *G. Rankinii.*]

RADFORD, A. E., H. E. AHLES, & C. R. BELL. Manual of the vascular flora of the Carolinas. lxi + 1183 pp. Chapel Hill, North Carolina. 1968. [*Gelsemium, Spigelia, Cynoctonum* (= *Mitreola*), *Polypremum, Buddleja,* 832–835.]

RECORD, S. J. American woods of the family Loganiaceae. Trop. Woods **56:** 9–13. 1938. [Includes *Buddleja* and five extralimital genera.]

RICKETT, H. W. Wild flowers of the United States. Vol. 2. The southeastern states. Part 2. vi + 323–688 [+ ii] pp. New York. 1966. [*Gelsemium, Spigelia, Polypremum, Cynoctonum* (= *Mitreola*), 388, 389, *pl. 139.*]

ROGERS, G. K. The taxonomic position of *Polypremum procumbens* L. (Loganiaceae). Am. Jour. Bot. **72**(suppl.): 967, 968. 1985. [Abstract of paper given at 1985 AIBS meetings.]

SMITH, L. B., E. F. GUIMARÃES, J. F. PEREIRA, & E. M. NORMAN. Flora ilustrada catarinense: Loganiáceas. 77 pp. Santa Catarina, Brazil. 1976.

SOLEREDER, H. Loganiaceae. Nat. Pflanzenfam. IV. **2:** 19–48. 1892; 49, 50. 1895. [For objections to the subfamilies recognized here, see especially KLETT (318); follows BENTHAM's (1846) subdivision of *Buddleja* and excludes *Nicodemia* and *Chilianthus*; includes illustrations of trichomes in *Polypremum*; calls attention to chlorophyll in seeds of *Spigelia*; for trichomes see also BENDRE (1973).]

———. Systematic anatomy of the dicotyledons. (English transl. from German by L. A. BOODLE & F. E. FRITSCH, revision by D. H. SCOTT.) Vol. 1. xii + 644 pp. Vol. 2. vi + pp. 645–1182 + errata. Oxford. 1908. [Loganiaceae **1:** 538–547; **2:** 989, 990; includes discussion of subdivision of the Loganiaceae.]

SOUKUP, J. Las Simplocáceas, Oleáceas, Loganiáceas y Desfontainiáceas del Perú, sus géneros y lista de especies. Biota **9:** 272–282. 1973. [Includes *Spigelia* and *Cynoctonum* (= *Mitreola*).]

STANDLEY, P. C. Loganiaceae. Trees and shrubs of Mexico. Contr. U. S. Natl. Herb. **23:** 1141–1147. 1924. [Includes *Gelsemium* and *Buddleja*.]

STEFFEY, J. The logania family. Am. Hort. **60**(8): 4, 6, 7. 1981. [Species of *Buddleja, Gelsemium, Spigelia, Strychnos,* and *Fagraea* from the horticultural standpoint.]

TAKHTAJAN, A. Outline of the classification of flowering plants (Magnoliophyta). Bot. Rev. **46:** 225–359. 1980. [Loganiaceae, in Gentianales, 292; Buddlejaceae, in Scrophulariales, 296.]

TAYLOR, N. Plant drugs that changed the world. viii + 275 pp. New York. 1965. [Strychnine, brucine, and curare from *Strychnos,* 46–48, 194–196.]

THORNE, R. F. Proposed new realignments in the angiosperms. Nordic Jour. Bot. **3:** 85–117. 1983. [Loganiaceae and Buddlejaceae, in Gentianales, 108.]

TIAGI, Y. D. Nodal and floral anatomy of Loganiaceae. Proc. Indian Sci. Congr. **58:** 512. 1971.*

——— & S. KSHETRAPAL. Studies on the floral anatomy, evolution of the gynoecium and relationships of the family Loganiaceae. *In:* Y. S. MURTY *et al.,* eds., Advances in plant morphology **1972:** 408–416. 1972 [1975]. [*Mitreola, Buddleja, Nicodemia,* and *Strychnos*; includes discussion of relationship between Rubiaceae and Loganiaceae (floral vasculature of *Mitreola* suggests Rubiaceae) and placement of Buddlejeae.]

TIREL-ROUDET, C. Loganiaceae. Fl. du Cambodge, du Laos et du Vietnam **13:** 3–89. 1972. [Includes *Gelsemium* (with distribution map for *G. elegans*) and *Mitreola*; Buddlejaceae treated separately by A. J. M. LEEUWENBERG & J. E. VIDAL, 90–97.]

TORREY, J., & A. GRAY. Rubiaceae suborder Loganieae. Fl. N. Am. **2:** 43–46. 1841. [Includes *Coelostylis, Mitreola,* and *Polypremum.*]

VINES, R. A. Trees, shrubs and woody vines of the Southwest. xii + 1104 pp. Austin, Texas. 1960. [*Gelsemium* (*G. sempervirens* in Oklahoma, but under *Gelsemium* see DUNCAN & DEJONG, who doubted this), *Buddleja,* and *Emorya,* 870–874.]

WAGENITZ, G. Die systematische Stellung der Rubiaceae. Ein Beitrag zum System der Sympetalen. Bot. Jahrb. **79:** 17–35. 1959. [Favors associating *Buddleja* with Scrophulariaceae, 19, 20.]

———. Loganiaceae. *In:* H. MELCHIOR, A. Engler's Syllabus der Pflanzenfamilien. ed. 12. **2:** 406–408. Berlin. 1964. [In order Gentianales, with six tribes; see MELCHIOR for Buddlejaceae.]

WEBERLING, F. Die Bedeutung blattmorphologischer Untersuchungen für die Systematik. Bot. Jahrb. **77:** 458–468. 1958. [*Buddleja,* 462, *fig. 3* (IV, V—leaf bases of *B.* "*variabilis*"); this species with "vaginale Öhrchen," which are found especially in families, including the Scrophulariaceae, that lack stipules; stresses that these should not be confused with stipules as in the Loganiaceae.]

WHERRY, E. T., J. M. FOGG, JR., & H. A. WAHL. Atlas of the flora of Pennsylvania. xxx + 390 pp. Philadelphia. 1979. [Includes *Buddleja alternifolia, B. Davidii, Polypremum procumbens,* all introduced, 287.]

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KEY TO THE GENERA OF LOGANIACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *Herbs, subshrubs, shrubs, or woody vines; stems usually with internal phloem (except Buddlejeae); leaves usually opposite, infrequently subopposite or whorled or pseudowhorled (alternate in the cultivated* Buddleja alternifolia*), simple and unlobed, usually with interpetiolar stipules or stipular flanges, rarely with one lobe at each side of the petiolar insertion, or stipules absent (*Buddleja Lindleyana*); inflorescences fundamentally cymose but otherwise diverse, lacking showy bracts; flowers actinomorphic or weakly zygomorphic, tetramerous or pentamerous; corollas tubular; stamens alternating with corolla lobes, epipetalous, uniform; anthers introrse, usually basally cleft; pollen grains usually colporate; ovary bilocular (or tetralocular in* Buddleja madagascariensis*); ovules many on axile or peltate-intrusive placentae; fruits capsules usually flattened contrary to the septum and dehiscing primarily septicidally and often loculicidally (berries in* B. madagascariensis*); seeds numerous; embryos straight.*

A. Plants usually twining vines, sometimes straggling shrubs; flowers externally bright yellow, over (2–)2.5 cm long, heterostylous; stigmatic lobes 4; fruits capsules over 1.2 cm long. . . . . 4. *Gelsemium.*

A. Plants usually herbs, subshrubs, or shrubs, rarely vines; flowers externally white, reddish, purplish, greenish, or rarely yellow (then less than 2 cm long), homostylous; stigmatic lobe(s) 1 or 2; fruits capsules less than 1 cm long or baccate.

B. Capsules markedly cleft into 2 rounded lobes at the apex, broader than long, dehiscing to leave behind a woody, cuplike remnant; calyx lobes between ⅙ and ⅓ the length of the corolla, linear, 5; style articulated. . . . . 1. *Spigelia.*

B. Capsules shallowly emarginate to acuminate at the apex (separating apically into 2 horns in *Mitreola*), longer than or about as long as broad, dehiscing variously without leaving a cupular remnant, or fruits baccate; calyx lobes under ⅙ or over ⅓ the length of the corolla, deltoid or ovate to rarely linear, 5 or 4; style not articulated.

C. Plants herbaceous; flowers usually either solitary between forks in stem or in cincinni; corollas white or pink; ovaries partly inferior.

D. Plants glabrous or with simple trichomes; leaves suborbicular to linear, over 4 mm wide; flowers in spikelike cincinni, pentamerous; capsule markedly 2-horned by apical separation of the carpels, apical lobes (horns) dehiscing adaxially only; style usually partly or completely torn lengthwise by separation of carpels. . . . . 2. *Mitreola.*

D. Plants with multicellular broadened trichomes; leaves almost linear, under 3 mm wide; flowers mostly solitary in forks between branches with some also in cincinni or other cymose arrangements, typically tetramerous; capsule emarginate to acute apically, separating at maturity into 2 stubby apical lobes, these dehiscing adaxially and usually abaxially as well; style not torn, remaining intact on 1 apical lobe. . . . . 3. *Polypremum.*

C. Plants usually shrubs, rarely vines; flowers in thyrsoid-paniculate arrangements; corollas usually purple, infrequently yellowish, greenish, pinkish, or white; ovaries superior.
E. Plants unarmed; leaves penninerved; trichomes stellate and/or glandular; flowers tetramerous; fruits usually capsular (berries in *B. madagascariensis*[3]). . . . . 5. *Buddleja.*
E. Plants armed with thorns; leaves with few arcuate lateral nerves ascending from the bases; trichomes simple; flowers pentamerous; fruits baccate. . . . . [*Strychnos spinosa.*[3]]

Tribe SPIGELIEAE Dumortier

1. **Spigelia** Linnaeus, Sp. Pl. **1:** 149. 1753; Gen. Pl. ed. 5. 74. 1754.

Annual or perennial herbs to subshrubs [or shrubs], sparsely to diffusely branched (often divaricately so). Stems tending to have pronounced longitudinal ridges; internal phloem present. Plants nearly glabrous or scabrous, or stems variably pubescent (mainly at nodes and along ridges), leaf blades (especially basally, along margins, and on veins), and sepals, bracteoles, and corollas slightly [to densely] pubescent also. Trichomes simple [or plants sometimes with a thick covering of "stellate hairs" composed of unicellular rays in tufts on pedestals]. Colleters present adaxially at bases of leaves, bracts, and (in some species) sepals. Leaves opposite or pseudowhorled, usually sessile or nearly so [or petiolate], the blades ovate to (mostly) lanceolate or elliptic [or suborbicular to linear], usually acuminate apically (to infrequently rounded), bases cordate to cuneate, secondary nerves often arcuate-ascending; stipules interpetiolar, membranaceous, blunt and broad to narrowly deltoid, sometimes marginally fimbriate. Inflorescences usually at ends of branches or in forks between branches, often with multiple peduncles or pedicels rising from one point, most species with spicate, branched, or unbranched cincinni, some with short monochasia, or with flowers paired or in small clusters with unequal pedicels radiating from one point, or flowers infrequently solitary; bracts and bracteoles subulate. Flowers pentamerous. Calyx lobes separate or basally connate, linear to narrowly lanceolate [to ovate] or narrowly deltoid, entire or minutely denticulate. Corollas diverse, white, purplish, reddish, or scarlet (yellow or yellow-green within in *Spigelia marilandica*), funnelform or with an elongate tube constricted at the throat, lobes shorter than the tube, valvate, usually pointed apically. Stamens included or exserted; anthers usually depositing pollen onto the pubescent subterminal shaft of the style. Ovary superior, with 2 apical lobes, each locule containing hemianatropous (*fide* Hakki) ovules inserted peltately on and partly embedded in a large, intrusive, peltate placenta inserted on the face of the septum (seen in *S. marilandica*); style much longer than ovary and stigmas, articulated above the base; stigmas unlobed or scarcely 2-lobed. Capsule strongly bilobed apically, somewhat flattened perpendicular to the septum, before dehiscence often crowned between the lobes with persistent base of style (this breaking off at articulation), both septicidal and loculicidal, circumscissile below, the segments separating from a persistent cupular

[3]Infrequently escaping from cultivation in Florida.

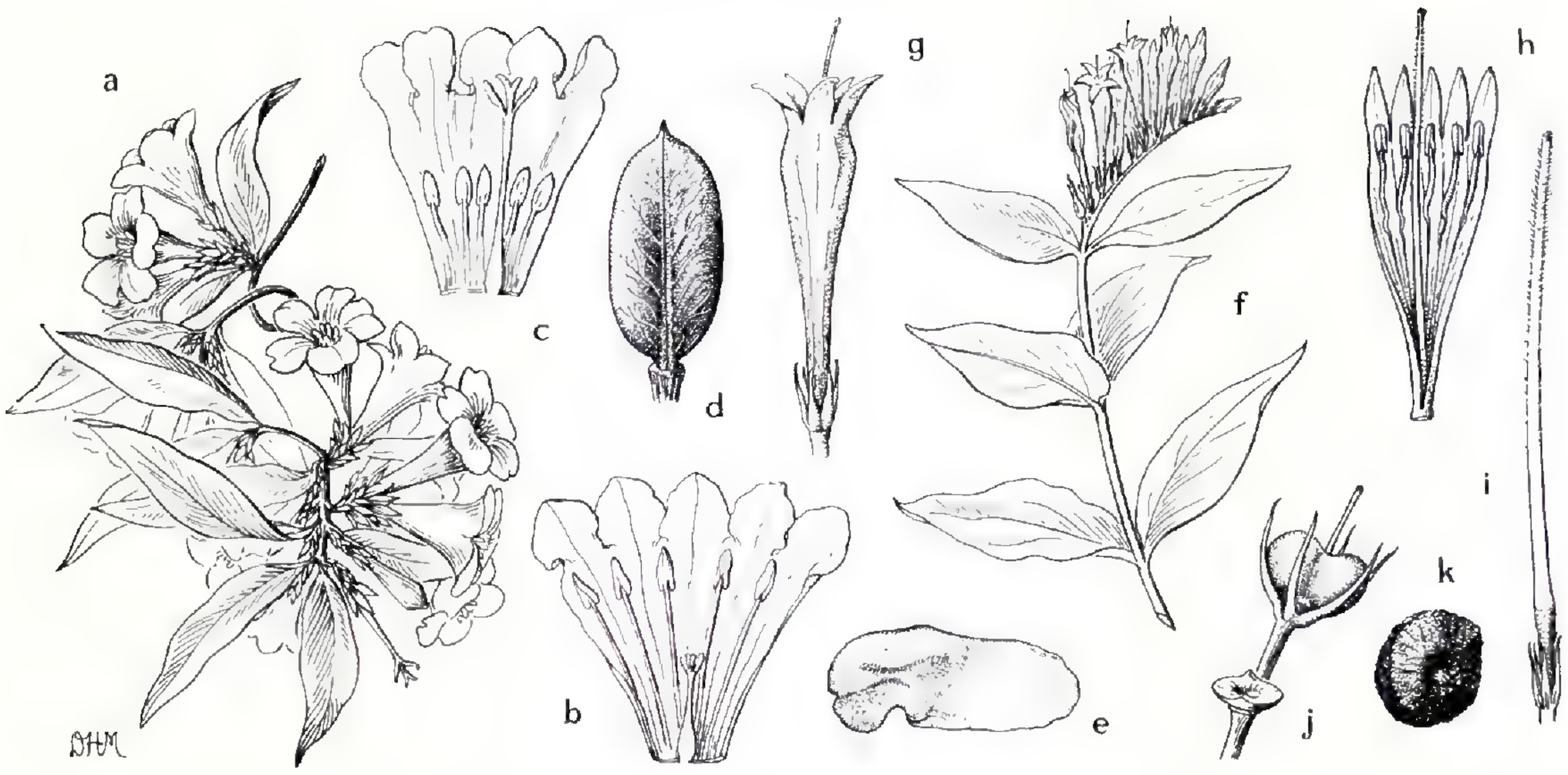

FIGURE 1. **Gelsemium** and **Spigelia.** a–e, *Gelsemium sempervirens*: a, flowering stem, × ¼; b, short-styled flower, opened, × ¾; c, long-styled flower, opened, × ¾; d, capsule, × 1; e, seed, × 2. f–k, *Spigelia marilandica*: f, flowering branch, × ¼; g, flower, × ¾; h, corolla, opened to show stamens and style, × ¾; i, gynoecium, showing basally jointed and apically pubescent style, × 1; j, capsule (with persistent sepals) and persistent fruit base (sepals removed), × 1; k, seed, × 3.

or boat-shaped, hardened base. Seeds verrucate or rugose, sometimes deeply pitted, usually dorsiventrally compressed, inserted peltately, angular to nearly circular (viewed from above). Endosperm initially nuclear, becoming ruminate by rapid growth into cavities formed by partial degeneration of integument. $2n = [26], 32, 48, [64]$. (Including *Coelostylis* Torrey & Gray ex Endl. & Fenzl.) TYPE SPECIES: *S. Anthelmia* L., the only species of the genus in the *Species Plantarum*. (Named for Paduan physician and author A. Spiegel, 1578–1625.)

Approximately 50 species distributed from the southern United States southward through Mexico, Central America, the West Indies (principally *Spigelia Anthelmia*), and South America to about the latitude of Buenos Aires, Argentina; the greatest number of species occurring in Brazil, but the genus absent or rare in the Amazon Basin. *Spigelia nicotianiflora* Chodat is disjunct between Mexico and Argentina-Paraguay (Hurley).

Earlier authorities set apart three of the six species of *Spigelia* in the southern United States as the former genus *Coelostylis,* which differs from our three other species of *Spigelia* most conspicuously in having usually white (vs. mostly reddish) flowers borne singly or in small pseudoumbellate clusters or short monochasia (vs. in spicate cincinni). One species formerly placed in *Coelostylis, Spigelia loganioides* (Torrey & Gray ex Endl. & Fenzl) A. DC., is a rare endemic in Levy, Marion, and Sumter counties, Florida, where it grows in low, moist, shady habitats, often calcareous hammocks, or elevations in river bottoms. Flowering takes place (April–)May through July. (For ecological details see Kral and Godfrey.) It is closely related to *S. texana* (Torrey & Gray) A. DC. *Spigelia texana* sensu stricto tends to be more branched and to have shorter corollas (usually 9.5–12 mm vs. generally over 12 mm in *S. loganioides*). It is endemic

to southern Texas in dry habitats, as well as in "swamp" and floodplain, and flowers (May–)June through August. The third species once segregated in *Coelostylis, S. Lindheimeri* Gray, often has a characteristic reticulation on the capsule and shorter, narrower leaves, a more compact habit (less erect and with internodes shorter than leaves), more basal branching, and smaller corollas (less than 1 cm long in Texas; to 13 mm in Mexican material) than the other species assigned to *Coelostylis. Spigelia Lindheimeri* inhabits relatively dry thickets and prairies in Texas and Mexico and flowers mostly from March through April in Texas—earlier than the other two species. As reflected by Hurley's broad but unpublished concept of *S. texana* encompassing all of the elements above, these three "species" are not easily distinguished and are in need of renewed study. The literature suggests that the seed coats may provide useful characters.

Of the three remaining species, *Spigelia marilandica* (L.) L., pinkroot, Indian pink, wormgrass, $2n = 48$, is the most widespread in our area and is recognized by its uniquely long (mostly 3.5–5.5 cm) tubular corollas that are scarlet on the outside and yellowish within. This species ranges from South Carolina and scattered localities farther north,[4] southward to northern Florida and west to southern Illinois, Missouri, Oklahoma, and Texas.

Spigelia marilandica seems to prefer rich soil at margins of or sometimes within woods but shows appreciable ecological amplitude, with its tolerances extending to rocky places. Its blooming period is from April (toward the south) into July or even October in the Big Thicket region of Texas (*fide* Ajilvsgi). *Spigelia marilandica* appears to be pollinated by the ruby-throated hummingbird, *Archilochus colubris* (L.) (see Austin).

Spigelia gentianoides Chapman ex DC. is most like *S. marilandica* but has shorter (less than 3.5 cm), pale pinkish or purplish corollas and included (vs. exserted) styles. Found in Jackson County (Kral) and reported once each from Washington, Calhoun, and Liberty counties (Godfrey) and Gadsden County (Hurley), western Florida, this rare species inhabits upland *Quercus-Pinus* woods (Kral) and flowers in May and June.

Our sixth species, *Spigelia Anthelmia* L., worm grass, $2n = 32$, has distinctively short (less than 1 cm) corollas and a pseudowhorl of large "bracts" beneath the inflorescence. The capsules are warty (vs. smooth, lineolate, or scabrous in our other species). Its distribution stretches from South America and the West Indies to Monroe and Dade counties, Florida, where it is weedy and colonial in hammocks, in cultivated places, and along roadsides. It is

[4]The present northeastern limit of *Spigelia marilandica* is most likely partly attributable to commercial collecting, cultivation, and habitat destruction. *Spigelia marilandica* has been recorded from—but is now rare or absent in—Pennsylvania (see Noll, Hurley; *cf.* Muhlenberg), Maryland (one unnumbered specimen at GH is labeled "Maryland" in Asa Gray's handwriting; see also Griffith; not listed in Boone as recently collected), Delaware (Hurley), New Jersey (Stone believed any presence to have resulted from introduction), Virginia (few reports—e.g., see Griffith; Hurley; Holm, 1892), and North Carolina (according to Youngken, once abundant; Stockberger mentioned it in 1907 as not common but present in low and middle districts of the state; the only specimen at A/GH is *Harbison s.n.*, Macon Co., North Carolina, 1899).

naturalized in Africa and in the Malay Archipelago. Leenhouts (1962) reported autogamy in this species.

Recognizing no formal infrageneric subdivisions, the De Candolles treated 33 species of *Spigelia* in the *Prodromus.* In the *Flora Brasiliensis,* Progel sorted 31 species into five sections that Solereder maintained in the first edition of *Die Natürlichen Pflanzenfamilien.* Except for Morelle and Bravo, who recognized a sixth section, modern authors, including Hurley, have ignored the sections, a practice probably best continued at least until the genus is revised again. In the meantime, new species accumulate, and the taxonomy leans heavily on regional treatments such as those of Bravo (Argentina), Smith (eastern South America), Smith and colleagues (Santa Catarina, Brazil), Guimarães & Pereira (Brazil), Macbride (Peru), Ewan (Colombia), Blackwell (Panama), Gibson (Guatemala), Alain (Cuba), and Gray (North America). An unpublished revision of *Spigelia* (1968) comprises a doctoral dissertation by Homer Hurley at George Washington University.

Distinguishing characteristics of *Spigelia* are noted in the family discussion.

The introrse anthers deposit pollen onto a pubescent section of the jointed style immediately beneath the short stigmatic lobes in most species.

Palynological data on *Spigelia* are sparse and contradictory. Observations show the grains usually to be (2-) 3- or (4-)colpate and suboblate or oblate and to have the tecta nearly psilate to shallowly undulate or verrucate and perforate, with the perforations scattered or in sunken clusters. Contradicting previous indications, Hoc & Bravo established colpus membranes as present, although easily destroyed by acetolysis. (Also see Erdtman; Punt, 1980; Punt & Leenhouts; and Melhem & Takahashi.)

"Spigeline," reported in the literature to be an alkaloid of *Spigelia marilandica* and other species, needs confirmation by modern techniques. Bisset (1980a) maintained that "nothing is known" of the nature of alkaloids in *Spigelia.*

Solereder (1892) called attention to chlorophyll in the seeds.

The outstanding use of several species of *Spigelia* is to expel parasitic worms. *Spigelia Anthelmia* and *S. marilandica* are both said to have served North American Indians as vermifuges, and both received substantial attention for the same purpose in 18th- and 19th-century scientific-medical journals. In the United States *S. marilandica* became a popular folk cure for worms among southern settlers and rose to temporary prominence in formal medicine. Two problems plagued its use. First, commercial collectors often adulterated and confused it with different species, the contamination remaining to this day a nuisance in the ample literature on the drug. The second problem is toxicity—*S. marilandica* and *S. Anthelmia* are both blamed for killing patients (and, as related by Morton, the latter has been used to kill fish, dogs, and criminals in South America). Symptoms of overdose include delirium, vertigo, speech abnormalities, convulsions, and troubles with the eyes: pain, dilated pupils, spasms, strabismus, and dim vision. Merely touching the South American *S. pedunculata* HBK. is risky, according to García-Barriga and Ewan. It is an ingredient in some curares and is used to kill domestic animals, fish, and insects (Hurley).

Spigelia splendens Hooker is a minor tropical ornamental.

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2. **Mitreola** Linnaeus, Opera Varia, 214. 1758.

Erect [or creeping] annual [or perennial] herbs or subshrubs, unbranched or branches ascending. Plants glabrate, scabrous, or puberulent [to pilose] on vegetative and reproductive organs, especially at nodes and on leaf veins and margins. Stems with internal phloem. Leaves opposite, sessile or on short petioles, the blades nearly linear to suborbicular, occasionally slightly succulent, the lateral nerves often arcuate. Stipules small and membranaceous, interpetiolar or inserted between sessile leaves, deltoid to forming a short transverse ridge [or acuminate], infrequently taking the form of 1 lobe at each side of the foliar insertion, such lobes connected by a ridge or rarely unconnected. Inflorescences usually pedunculate, tightly condensed to uncrowded, made up of straight or curled, spicate, cincinnous branches, these in cymose arrangements (usually with multiple orders of branching, the branches often unevenly pseudoumbellate or in dichasial pairs, or sometimes arising laterally from a well-defined determinate central axis). Flowers sessile or on short pedicels, pentamerous, each opposite a lanceolate to subulate bract and associated with an inconspicuous bracteole (not consistently discernible). Calyx lobes separate or basally coalescent, elliptic to ovate or deltoid, rounded to acuminate apically. Corolla white or infrequently pinkish [to violet], when dry usually with dark longitudinal veins and/or with the base purplish and the lobes creamy, urceolate, slightly exceeding to about 4 times longer than calyx, pilose in the throat, the lobes ca. ¼–⅔ the length of the corolla, valvate or imbricate, oblong or tapered from or just above the slightly contracted base to the rounded or acuminate apex. Stamens inserted near the base of the corolla tube; filaments about as long as or shorter than the stubby, usually cordate, dorsifixed anthers; pollen small, 3-colporate, psilate (*M. petiolata* and a few other species). Ovary partly inferior, the ovules on an expanded, stalked [or sessile?] placenta; carpels initially separate apically or separating apically, although joined at the style; style usually splitting partly or completely lengthwise by the carpellary separation or remaining intact, linear and short [or absent]; stigma knoblike. Capsule 2-horned (when style splits completely) [or capsules nearly spherical and only slightly bilobed apically]; each horn straight or bowed outward, about ⅓ to over ¾ the length of the capsule, dehiscing longitudinally along the adaxial face (toward the other horn), often papillose, ovate or pyriform in abaxial view, rising to a usually pointed or truncate apex crowned with a half style (when this has split completely and when style is not borne intact on 1 horn) [or crowned with half stigma when style absent]. Seeds minute, reticulate, warty,

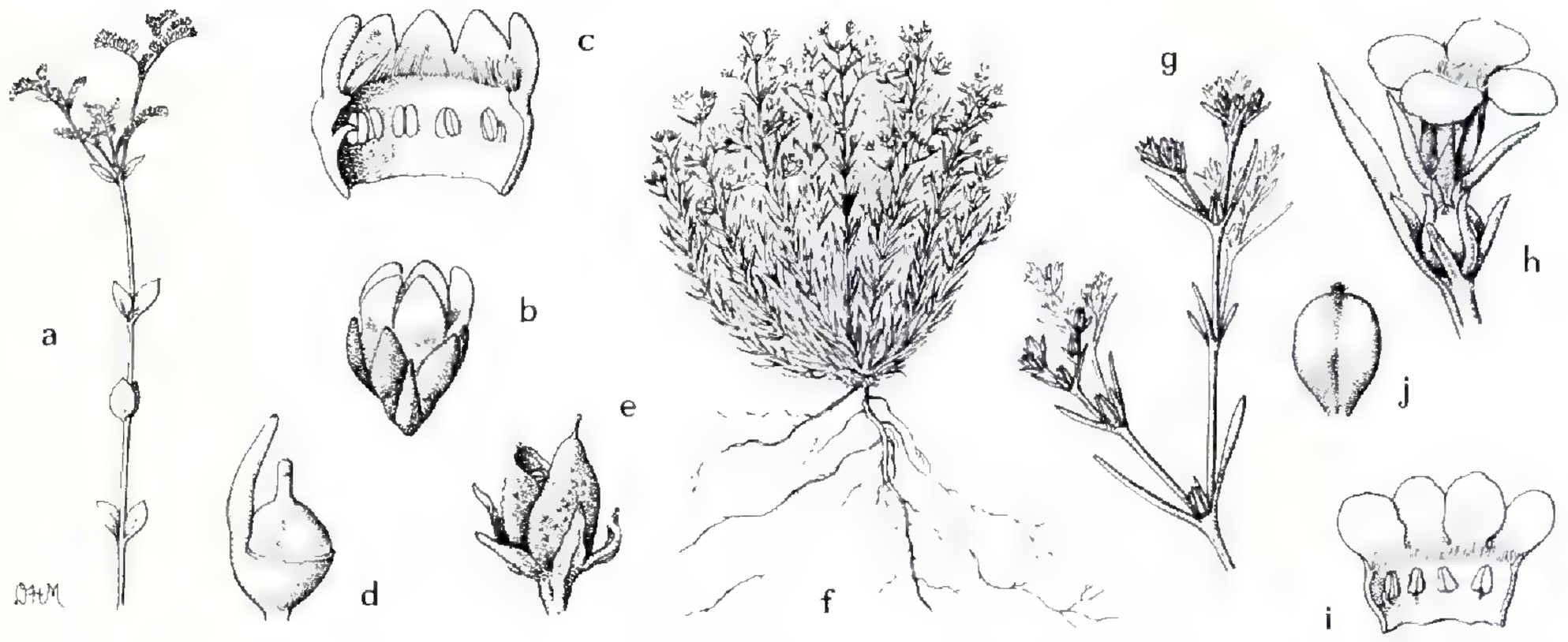

FIGURE 2. **Mitreola** (*Cynoctonum*) and **Polypremum.** a–e, *Mitreola sessilifolia*: a, habit, × ¼; b, flower, × 4; c, corolla, opened to show stamens and pubescent throat, × 6; d, gynoecium, showing intact style, all but 1 sepal removed to show point of attachment, × 8; e, capsule, carpels separated apically into 2 lobes, these dehisced vertically along inner (adaxial) faces (1 visible), × 5. f–j, *Polypremum procumbens*: f, habit, × ¼; g, branch, × 1; h, flower and subtending leaves, × 4; i, corolla, opened to show stamens and pubescent throat, × 3; j, undehisced capsule bearing remnant of style, × 5.

or unsculptured, attached peltately, ventrally grooved or dented, dorsally rounded, elliptic [to fusiform] in outline. Embryo nearly linear. (*Cynoctonum* J. F. Gmelin, Syst. Nat. ed. 13. **2**: 306, 443. 1791, not E. H. F. Meyer, 1838.) TYPE SPECIES: *Ophiorrhiza Mitreola* L. = *Mitreola petiolata* (J. F. Gmelin)[5] Torrey & Gray, the only species known to Linnaeus. (Name diminutive of Latin *mitra,* miter, from the twin-peaked capsule.)—MITERWORTS, HORNPODS.

In Leeuwenberg's revision of *Mitreola,* he recognized six species: *M. pedicellata* Bentham (northern India and neighboring regions), *M. reticulata* Tirel (North Vietnam), *M. sphaerocarpa* (Leenh.) Leenh. (Borneo), *M. turgida* Jovet (Madagascar), and the two species in the United States. Li added a seventh species, *M. petiolatoides,* from Yunnan Province, China.

Mitreola petiolata (*Cynoctonum petiolatum* J. F. Gmelin, *C. Mitreola* (L.) Britton, *C. succulentum* R. W. Long), $2n = 20$, is distributed in warm parts of Australia, Asia, western Africa (see Heine), South and Central America, the West Indies, southern California, and much of the southeastern United States in an area defined by southeastern Virginia, Tennessee, southeastern Missouri,

[5]Gmelin cited no specimens and adopted the epithet for *Cynoctonum petiolatum* from the invalid and untypified *Anonymos petiolata* Walter. Authors have turned for a type to the Gronovius herbarium, which contains material linked to Linnaeus's different epithet for the same species (see annotations under Gronovius and Dandy, 1958). Leeuwenberg's (1972) citation of a "type" for *Mitreola petiolata* from Gronovius's herbarium might be broadly interpreted as the selection of a neotype, except that he later (1974, p. 9) stated in connection with the basionym, "Type apparently not preserved, not in the Walter herbarium in BM." Also in 1972, Tirel-Roudet evidently designated as "type" the same specimen as Leeuwenberg's "type" from the same year: "Virginie, *Clayton s. n.* in herb. Gronovius (BM!)."

southern Oklahoma, central and eastern Texas, and Florida. It is mainly a plant of the Coastal Plain.

In our area *Mitreola petiolata* generally prefers open or sometimes shady and usually wet habitats (but see discussion of *Cynoctonum succulentum* below). *Mitreola petiolata* occupies shores, marshes, hammocks, floodplains, ditches, pine savannas, swamps, swales, and abandoned fields. Its flowering period spans the entire year in Florida but becomes restricted to late summer or early autumn toward the north.

Long separated his new *Cynoctonum succulentum* from *Mitreola petiolata* (*C. Mitreola*) by its shorter inflorescences, shorter petioles (or virtually none), thicker leaves differing in shape, reduced branching, basal rosettes, and greater tolerance for drier locations in pine woods (although not to the exclusion of moist areas). Dismissing the materials of *C. succulentum* that he had examined as "vigorous young specimens of *M. petiolata*" (p. 19), Leeuwenberg (1974) denied it any formal status in his revision. That he came across "similar specimens" from Puerto Rico and Jamaica suggests that *C. succulentum* may not be endemic to southern Florida as Long thought.

The short-petioled, sometimes small, thickened leaves, minimal branching, and congested inflorescences of *Cynoctonum succulentum* approach the second universally recognized species in the southeastern United States: *Mitreola sessilifolia* (J. F. Gmelin) G. Don (*C. sessilifolium* J. F. Gmelin, *M. angustifolia* (Torrey & Gray) J. Nelson). *Mitreola sessilifolia* grows chiefly on the Coastal Plain from southern Virginia to eastern Texas but has been collected in New Mexico, southern Oklahoma, and the Bahamas. It is most often found in damp, open or partly open habitats, such as moist spots in pine woods, cleared land, swamps, marshes, shores, and ditches. Collectors often describe the sites as "grassy." In the southeastern United States, *M. sessilifolia* flowers from early summer (but as early as February toward its southern limit) through early autumn. Sessile or subsessile leaves, more congested inflorescences, and capsules more often abaxially verrucose differentiate it from *M. petiolata*. However, the boundary is sufficiently blurred for both Leeuwenberg (1974, stressing seed coats) and Long to have acknowledged the plausibility of hybridization or "introgression." I find certain specimens difficult to place in one species or the other.

Mentioning ecological differences, Long (see also Long & Lakela) established *Cynoctonum sessilifolium* var. *microphyllum* for specimens with short (mostly under 1.5 cm vs. over 2 cm), comparatively narrow leaves having acute (vs. obtuse) apices, simple stems, and inflorescences bearing few, short branches. The distribution of this putative variety nearly matches that of var. *sessilifolia*. To back up his refusal to recognize it, Leeuwenberg (1974) cited continuity of variation in leaf size and remarked on the great differences in this character within the type collection of *Mitreola sessilifolia*. The pattern of variation in sizes and shapes of leaves on specimens in the Harvard Herbaria (A and GH) does indeed weaken the concept of var. *microphyllum*.

Torrey & Gray assigned specimens having narrowly elongate and "closely sessile, obscurely veined" leaves to *Mitreola sessilifolia* var. *angustifolia* (*Cynoctonum angustifolium* (Torrey & Gray) Small, *M. angustifolia* (Torrey &

Gray) J. Nelson), which grows in Florida and on the Coastal Plain of Georgia. Specimens of this possible variety in the Harvard Herbaria have stipular flanges with edges either straight and horizontal or notched at the middle, whereas in other possible varieties the edges usually rise at the middle. Moreover, the abaxial lateral nerves of leaf blades of var. *angustifolia* are usually sunken or less prominent than in the rest of the species. As might be surmised by its occasional elevation to a species, var. *angustifolia* is more distinctive than var. *microphyllum* (*microphylla*), but Leeuwenberg (1974) thought it insufficiently distinct for recognition.

Mitreola petiolata forms vanillic and ρ-coumaric acids, according to Daniel & Sabnis.

Mitreola is economically inconsequential. Roots from *M. petiolata* have served in folk treatments for snake bites and worms.

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3. **Polypremum** Linnaeus, Sp. Pl. **1:** 111. 1753; Gen. Pl. ed. 5. 50. 1754.

Procumbent to ascending, matted to scoparioid, perennial or reportedly sometimes annual, taprooted, heliophilous herbs. Plants made up of 1 (infrequently) to innumerable (frequently) vegetative and fertile stems arising as a result of often highly congested basal branching; branching lateral (particularly toward the base of the plant) and usually pseudodichotomous-dichasial (especially distally on the plant). Tufts of short vegetative stems and associated foliage often forming dense overwintering rosettes. Plants usually scabrous-serrulate along leaf margins and frequently so on stem ridges, midribs of leaves, and sepals, also with minute, sunken hairs made up of a basal cell, a stalk cell, and usually 4 (but occasionally 8) cells comprising a broadened cap. Branchlets fluted, often with 4 sharp flanges and 2 or 4 rounded ridges, containing palisade tissue and lacking internal phloem. Leaves opposite, sessile, joined basally by a transverse membrane, the blades virtually linear, gradually tapered to acuminate apices, usually widest near or somewhat above the middle, sometimes

broadening gradually toward the base, the midribs usually prominent abaxially, other vasculature inconspicuous, containing palisade tissue on both sides. Flowers borne singly between pseudodichotomous branches, also clustered in various cymose arrangements, these usually dichasial and occasionally with cincinnoid or scorpioid branches, or infrequently the entire inflorescence variously monochasial. Flowers tetramerous or infrequently pentamerous, very rarely with 6 calyx lobes, subtended by a reduced pair of foliage leaves ("bracteoles"). Calyx lobes connate basally, lanceolate, with hyaline margins, the attenuate apices continuing the thickened and abaxially keeled midribs. Corolla white, shorter than to exceeding the calyx, cruciform-salverform, with a ring of hairs in the throat, the spreading, subequal lobes oblong to obovate, rounded to truncate apically, ⅓–⅔ the length of the corolla, imbricate. Filaments approximately as long as anthers, these cleft at both ends, dorsifixed, broadest near base; pollen grains oblate-spheroidal, tricolporate, the tectum psilate-perforate. Ovary partly inferior, flask shaped (including the style), compressed perpendicular to the septum, the ovules amphitropous (inserted transversely at middle of funiculus) or (*fide* Hakki) anatropous, on a narrowly oblong placenta inserted near the base of the septum; style very short; stigma capitate, unlobed or nearly so, papillose, about as long as style. Capsule nested in the persistent calyx, small (ca. 2 mm long), compressed, obovate to ovate, usually elliptic, septum forming a sunken vertical line, emarginate to acute at apex, there separating septicidally into 2 adaxially and longitudinally opening lobes, also usually opening along abaxial sutures, the stubby remnant of style remaining intact on 1 lobe. Seeds translucent yellow when dry, minute, irregularly polygonal, roughly isodiametric, not sculptured or faintly reticulate-rugulose. Endosperm initially cellular. Embryo stocky, the thickened cotyledons about ⅓ its length. (*Hasslerella* Chodat.) TYPE SPECIES: *Polypremum procumbens* L. (Name from Greek *polys,* many, and *premnon,* stem.)

A genus of a single weedy species distributed in South America (there nearly restricted to the north), Central America, Mexico, the West Indies, and the United States. While the northern limit probably fluctuates, most natural populations in the United States fall within the area defined by the Florida Keys, the eastern two-thirds of Texas, Oklahoma, southeastern Missouri (and collected once in the northeastern corner of this state), Tennessee, and North Carolina. *Polypremum* has been collected but is now rare or perhaps absent in southwestern Kentucky (V. Bates, pers. comm.), southern Illinois (Mohlenbrock), and southeastern Indiana (Collins). Its range extends along the Atlantic coast to Delaware and Maryland, with a few scattered collections from farther north: southeastern Pennsylvania (in Wherry *et al.* as introduced) and adjacent New Jersey (Camden, *C. F. Parker,* 9-21-1865, GH, "in ballast sand"). Miller encountered *Polypremum* on Long Island, New York.

Chodat's genus *Hasslerella,* a synonym of *Polypremum,* is based on a disjunct population in Paraguay (see Pennell). An old report of *Polypremum* in Chile is probably erroneous. Outpost populations in Hawaii, Guam, Wallis (near Samoa), and Palau (localities from Fosberg and Fosberg & Falanruw; specimens at US!) probably originated from recent introductions. Others certainly must exist.

Polypremum inhabits wet or more often dry, usually open localities at both low and high altitudes, mainly on sandy soil or even on bare sand. Favored habitats include *Pinus* savannas, other open woods, artificially disturbed places, shores, edges of swamps or woods, ditches, marshes, prairies, and littoral dunes.

Polypremum flowers mostly from late spring through early autumn in our area, but dates on flowering specimens from Florida cover nearly the entire year.

Three embryological attributes of *Polypremum* struck Moore (1948) as peculiar: the megagametophyte invades the micropylar canal to the ovular surface; the zygote moves from a point of origin in the micropyle to the center of the endosperm; and short, cylindrical, possibly haustorial "necks" protrude from both ends of the endosperm. In addition, the inner wall of the inner epidermis (an endothelium) thickens in the seed coat.

Moore (1947, 1948) counted $2n = 22$ and $3n = 33$ using roots and endosperm from *Polypremum procumbens* collected in North Carolina. His use of sectioned material makes verification desirable. The data on one herbarium specimen from Guyana (*K. R. Robertson & D. F. Austin 269,* 1967 (GH)) give $2n = 20$. Moore's illustrations show heterogeneous chromosomes intergrading in length.

The relationships of the genus are discussed under the family treatment.

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Tribe GELSEMIEAE G. Don

4. **Gelsemium** A. L. de Jussieu, Gen. Pl. 150. 1789.

Woody, twining, climbing or sometimes creeping, perennial vines (individuals of *Gelsemium sempervirens* with leafless runners when traversing areas of bare rock), or occasionally shrubby. Adventitious roots forming on rhizomes. Stems with internal phloem (seen in *G. sempervirens*). Plants glabrous or puberulent-hispidulous on axes (particularly at nodes), petioles, basal portions of foliar midribs, and (in *G. Rankinii*) often mid-basal portions of abaxial leaf blades. Leaves opposite or whorled, petiolate, the blades mostly narrowly lanceolate to elliptic or ovate, rarely linear, usually acuminate apically, cuneate to truncate basally. Petiole bases usually connected by a stipular flange, with colleters axillary and between petioles. Flowers solitary on pedicels in leaf axils or in axillary or terminal pairs or clusters often composed of a short, bracteate, determinate central axis bearing pedicellate flowers or branch axes, sometimes multiple pedicels or peduncles arising in 1 axil. [In *G. elegans* inflorescences large compound cymes usually with well-developed central axes.] Pedicels bearing 1 to many deltoid to ovate or lanceolate, often ciliate bracteoles, frequently associated with colleters. Flowers showy, pentamerous, heterostylous [or homostylous], fragrant or not. Sepals separate, oblong-elliptic to ovate or deltoid, rounded to acuminate apically, often ciliate, caducous or persistent. Corolla yellow or orange [sometimes with red markings in *G. elegans*], funnelform, actinomorphic to slightly zygomorphic, lobes imbricate, mostly ⅕–½ the length of the tube, rounded to obtuse [to acuminate] and sometimes apiculate or emarginate apically. Stamens inserted at base of corolla tube; anthers connivent or separate, sagittate; pollen grains usually nearly spherical to prolate, tricolporate, the endoapertures with distinct margins and 2 lateral extensions, tectum striato-reticulate (based on Punt, 1980). Ovary bottle shaped, gradually tapered to style, containing anatropous ovules (*G. sempervirens*) on axile placentae; stigmas twice forked into 4 papillate lobes. Capsule flattened perpendicular to septum, septicidal and loculicidal, splitting partly or completely into 4 segments, elliptic or oblong in outline, beaked with persistent style base [or beak absent]. Seeds flat, irregular in outline, with a thin, tawny wing at 1 end (*G. sempervirens*) or wing absent (*G. Rankinii*) [or seeds surrounded by an erose wing in *G. elegans*]; embryo nearly cylindrical but slightly spatulate (*G. sempervirens*). TYPE SPECIES: *Bignonia sempervirens* L. (= *Gelsemium sempervirens* (L.) Jaume St.-Hil.) (Generic name dating back at least into the seventeenth century; Italian, Medieval Latin, and archaic English words for jasmine are similar to *Gelsemium*; name ultimately probably from Arabic or Persian *yasmin* or similar words for jasmine (*Jasminum,* Oleaceae) possibly combined with Italian *gèlso,* for species of *Morus.*)

A genus of three species distributed in southeastern North America, Central America, and Asia. (See Ornduff, who revised *Gelsemium* and studied its reproductive biology.)

Gelsemium sempervirens, Carolina jasmine, yellow jessamine, or yellow jasmine, ranges from southeastern Virginia southward to (mostly northern) Florida and westward to Tennessee, Arkansas, eastern Texas, and perhaps (as in Vines but not other sources) Oklahoma. Disjunct populations occur in southern Mexico and Guatemala. Its ecological tolerances are broad—reported habitats include dry, sandy soil, savannas, pine barrens, rock outcrops, thickets, hardwood forests, hammocks, edges of salt marshes, dune hollows, boggy areas, shady creek bottoms, and swamps. Godfrey & Wooten (p. 516) mention "lowland woods where water stands only for short periods." In our area *G. sempervirens* blooms mostly from (January or) February through April (or early May toward the north) and infrequently in autumn (or rarely at other times). Most seeds are dormant for two years (Speer).

Beyond ecological and phenological differences, the second species in our area, *Gelsemium Rankinii* Small,[6] differs from *G. sempervirens* in its acuminate, persistent, nonciliate sepals (vs. sepals less sharply pointed to rounded, deciduous, and usually ciliate); pedicels with few, nonciliate bracteoles (vs. pedicels covered with ciliate bracteoles); wingless seeds (vs. seeds winged at one end); usually scentless flowers; and more pubescent petioles. Hybridization between *G. Rankinii* and *G. sempervirens* is strongly inhibited (Ornduff, 1970), which is not surprising since they grow close together in some places (occasionally leading to mixed collections).

Gelsemium Rankinii is nearly totally confined to wet habitats on the Coastal Plain from North Carolina to eastern Louisiana, except for southern Florida. It flowers slightly later than the preceding species, mostly in March and April, although as early as January toward its southern limit, and infrequently in September and October.

The Asian *Gelsemium elegans* (Gard. & Champ.) Bentham (*Leptopteris sumatrana* Blume) differs from the American species in its large, elaborate inflorescences (vs. flowers solitary or in small clusters), its smaller flowers tending to have pointed (vs. rounded) corolla lobes, its less flattened capsules, and its

[6]From the three herbarium sheets that bear specimens of *Gelsemium* in Michaux's herbarium, Ornduff (1970) accepted as the holotype of *G. nitidum* Michaux (Fl. Bor. Am. **1:** 120. 1803) the only one evidently thus labeled by Michaux. Holotype status for this specimen is debatable, however. "A holotype is the one specimen or other element used by the author or designated by him as the nomenclatural type" (ICBN, Art. 7.3). Michaux cited no specimens when *G. nitidum* was published, and he appears to have used materials other than the alleged holotype, since the floral details in his description are unlikely to have come from this evidently fruiting specimen. (Seen only on fiche 29 of IDC micro-edition; buds or damaged flowers may be present.) Several flowers in good condition are on one of the two other herbarium sheets. A second problem is that the sheet in question appears to consist of a mixture of *G. sempervirens* and *G. Rankinii.* If so, the use of this specimen for a lectotype requires choosing the material (species) on it that corresponds best with the original description of *G. nitidum,* which could threaten the more recent name *G. Rankinii.* Recognizing the ambiguities, Ornduff suggested dismissing *G. nitidum* as a *nomen confusum* to be placed in the synonymy of *G. sempervirens* because of Michaux's characterization of floral scent in the protologue of *G. nitidum.* (However, floral scent is not unknown in *G. Rankinii*—see Duncan & Dejong.)

seed surrounded by a wing. It grows in southern China, Burma, Thailand, Laos, Vietnam, India (Assam), Borneo, and Sumatra.

Gelsemiums are recognized as trailing or climbing vines or straggling shrubs with large, showy, yellowish, infundibular, heterostylous (ours), often fragrant flowers with sagittate anthers and four-parted styles. The seeds are flat, and they are winged in two of the species. The capsules are compressed perpendicularly to their septa.

Most modern authors pair *Gelsemium* with *Mostuea* Didr. as (or in) the tribe Gelsemieae. Both *Gelsemium* and *Mostuea* have heterostylous flowers (except races of *G. elegans*), four stigma lobes, and similar indole alkaloids (sempervirine and probably gelsemine are shared) and pollen. *Gelsemium* differs from *Mostuea* in its chromosome number ($2n = 16$, vs. 20), nonvestured pits in the vessel elements, oblong-elliptic (vs. usually bilobed) capsules containing many (vs. one or two) seeds per locule, and yellow or partly red (vs. usually mostly white) corollas. (See Ornduff, 1970; Bisset *et al.*; Punt, 1980; Leeuwenberg & Leenhouts; Mennega; and Saxton.)

Gelsemium sempervirens is unusual anatomically in that a cambium and secondary xylem form between the intraxylary phloem and the primary xylem (Solereder, 1908).

Aspects of the breeding system of *Gelsemium* elucidated by Ornduff (1970, 1979, 1980) include its pollination mostly by large-bodied bees (although small bees visit *G. sempervirens*) and its heterostyly that is associated with a self-incompatibility system within each morph in both American species.[7] Ornduff also showed that some races of *G. elegans* are homostylous, while others are heterostylous; that in *G. sempervirens* pin flowers are homozygous recessives at one locus, thrums heterozygous; and that in *G. sempervirens* intrafloral pollen transfer is appreciable. Corollas of *G. sempervirens* show pronounced ultraviolet patterns with light lobes (reflecting) and dark tubes (absorbing) (see photos in Eisner *et al.*).

Gelsemium sempervirens is a favorite, often-cultivated, wild flower in the southeastern United States and is the state flower of South Carolina. Highly bioactive, it was once prominently used as folk and formal remedies, which in overdoses no doubt killed more patients than it saved. (Medicinal applications of *Gelsemium* are discussed in Holm, Holmes, Lloyd, and Speer.) It remains a peril to livestock and to children who suck nectar from or eat the flowers (see Morton, Blaw *et al.*). The nectar is reputedly poisonous to young bees (Gowanloch & Brown) and may have been the source of the toxin in honey that killed three people in South Carolina (as related by Chesnut, who remained skeptical that *Gelsemium* was at fault). Also used medicinally and said to poison visiting insects, *G. elegans* has been an instrument of murder, execution, and suicide in Asia (Bell, Chesnut, Ford *et al.*). When eaten, *Gelsemium* inhibits synaptic activity of motor neurons (Perkins & Payne). Symptoms include weakness and paralysis, drooping of the jaw, staggering, ptosis, visual disturbances, slurred speech (or inability to speak), dilated pupils, feeble (or abnormal) heart-

[7]Heterostyly may be principally an adaptation that minimizes inappropriate pollen deposition in plants already having incompatibility systems (see Proctor & Yeo).

beat, convulsions, and (in certain cases death by) respiratory paralysis. (Consult Chesnut, Blaw *et al.*, Hardin, Holmes, and Perkins & Payne for details.) *Gelsemium sempervirens* also causes dermatitis (McCord).

Indole alkaloids are responsible for the toxicity of these plants. *Gelsemium sempervirens* contains sempervirine, yohimbine and/or derivatives (Neuss), gelsemine, gelsemicine (the principal poison), gelsedine, and gelsevirine (sometimes spelled "gelseverine"). Similar alkaloids, including sempervirine, gelsedine, gelsevirine, and gelsemine, have been isolated from *G. elegans*. Because the literature on alkaloids in *Gelsemium* is extensive, beset with nomenclatural confusion, and chemically complex, Saxton's monographic review is especially helpful. (Also see Bindra; Bisset, 1980a; Cueilleron *et al.*; Jin & Xu; Kisakürek *et al.*; and Yang & Chen, 1982a, 1982b, 1983.)

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Tribe Buddlejeae Bentham[8]

5. **Buddleja** Linnaeus, Sp. Pl. **1:** 112. 1753; Gen. Pl. ed. 5. 51. 1754.

Sarmentose subshrubs, climbers (*Buddleja madagascariensis*), or usually shrubs [or herbs or trees]. Plants with stellate and sometimes candelabrum-shaped trichomes with 4 or more rays per whorl, the trichomes frequently forming a felt on the abaxial side of leaf blades (these rarely glabrate), petioles, and young axes, very dense to absent on adaxial leaf surface and calyx, and absent to felted externally on corolla. Calyx and corolla with dense to sparse or absent, amber to white, often glistening (when dry), glandular hairs externally with 2-or-more-celled swollen heads on short stalks, such hairs sparse or absent on vegetative organs. Twigs angled or terete, internal phloem absent. Leaves petiolate [or sessile, sometimes perfoliate], opposite or subopposite [rarely alternate], ovate, lanceolate or elliptic, often quite narrow [or linear and extremely short], acuminate to long-attenuate at the apex, the base subcordate to more often cuneate or caudate, margins entire, sinuate, crenate, or serrate [or lobed]; stipules interpetiolar, thick and green (when living), blunt, or absent. Inflorescences terminal or infrequently lateral, usually cylindrical or narrowly conical thyrses (but the long main axis at least sometimes determinate), the lateral units infrequently single flowers, more often simple or compound, sometimes congested and fasciculate dichasia [or arranged into spherical heads or series of pseudoverticils in some species], branch axes resembling the primary axis in specimens of *B. madagascariensis*; flowering branches smaller than the main inflorescence, commonly arising from upper leaf axils; basal bracts intergrading with foliage leaves or sharply reduced, distal bracts and bracteoles linear or narrowly deltoid. Flowers sessile or on short pedicels, actinomorphic or nearly so, tetramerous [very rarely pentamerous], perfect or with anthers or gynoecium sterile, sterile organs resembling the functional organs or reduced. Calyx tubular, cylindrical or flared or urceolate, frequently about as long as the corolla lobes, topped with deltoid teeth less than $\frac{1}{10}$–$\frac{1}{3}$ (to ca. $\frac{1}{2}$) the length of the calyx. Corolla usually purplish (*B. Lindleyana, B. Davidii,* often with an orange center in the latter, some cultivars of this with white, pinkish, or nearly red corollas) or yellowish or pale orange (*B. madagascariensis*), salverform or infundibular, sometimes curved, with a long, narrow, cylindrical or slightly flared tube [or the tube hemispheric], pubescent within (only at the base in *B. madagascariensis*), the lobes less than $\frac{1}{10}$–$\frac{1}{3}$ (or ca. $\frac{1}{2}$) [or exceeding] the length

[8]Although cited by some authors as the authority for this tribal name, Bartling published Buddlejea as a subgroup of undesignated rank under ordo Scrophularinae in his *Ordines Naturales Plantarum* (1830). Bentham published Buddleieae as a tribe on June 1, 1835, according to a statement printed at the base of an associated plate (*Bot. Regist. pl. 1770*). If June 1 is correct, Bentham's publication antedates David Don's tribe Buddlejeae in the July issue (vol. 19, p. 111) of the *Edinburgh New Philosophical Journal* of the same year.

of the tube, erect or spreading, obovate to ovate, frequently elliptic-oblong, sometimes broader than long, rounded or truncate apically, imbricate [or valvate], the margins entire or crenate-erose. Stamens inserted below middle of corolla tube to near the mouth; anthers included [or exserted], dorsifixed, cleft at the base, oblong or broadened basally [to almost orbicular], longer than the filaments [except in sect. CHILIANTHUS]; pollen variable, 3- or 4- [or 8-]colporate, the exine smooth, punctate [or reticulate]. Ovary superior, with 2 or 4 (*B. madagascariensis*) locules, nearly cylindrical or turbinate and somewhat compressed (or almost spherical in *B. madagascariensis*), containing anatropous or hemianatropous ovules on elongate axile [or partly parietal] placentae (these attached at the apex of the septum in *B. Davidii*); style about as long as ovary (or much longer in *B. madagascariensis*), included [or exserted]; stigma elongate and narrow to globose. Fruits fusiform to ovoid, primarily septicidal but also apically loculicidal capsules (*B. Davidii, B. Lindleyana*) or berries (*B. madagascariensis* and others of sect. NICODEMIA), surrounded by the persistent calyx. Seeds minute, fusiform-linear (*B. Davidii*) or polygonal, with or without a narrow, irregular wing (*B. Lindleyana*), or unwinged and ovoid to ellipsoid (*B. madagascariensis*). Endosperm initially cellular. (Including *Adenoplea* Radlk., *Nicodemia* Ten., and *Chilianthus* Burchell.) TYPE SPECIES: *B. americana* L., the only member of the genus in the *Species Plantarum.* (Named for British clergyman and botanist Adam Buddle, ca. 1660–1715.)—BUTTERFLY BUSH.

A genus of some 100 species (Norman, pers. comm.) in tropical and subtropical (and, to a limited extent, warm-temperate) Asia, the Arabian Peninsula, eastern and southern Africa, Madagascar, the Mascarene Islands, and America. Centers of diversity are in and about south-central China, including the eastern Himalayas, and tropical America. Roughly one-third of the species occur in the Old World. The widespread *Buddleja asiatica* Lour. occurs across most of southern Asia, and the range of *B. americana* reaches from northern Mexico to the West Indies and Bolivia. Fifteen species are indigenous to Mexico, and five to the southwestern United States. Of the handful of alien species cultivated in this country, three persist or spread from plantings in the range of the Generic Flora.

Section NEEMDA Bentham is represented in the southeastern United States by *Buddleja Davidii* Franchet, $2n = 76$, and *B. Lindleyana* Fortune, $2n = 38$. The former, the best-known species of the genus, is indigenous to China and possibly Japan. Being hardy and popular in gardens, it turns up adventively in scattered regions, such as much of Europe, where it colonized rubble left after the Second World War. The spotty distribution of *B. Davidii* in the United States includes mostly, but not exclusively, the states along the mid-Atlantic seaboard. It may be encountered in our area on disturbed ground, along roadsides, on shores, and in rocky places. Norman (pers. comm.) adds that it readily escapes from cultivation around Seattle, Washington. The natural polymorphism of *B. Davidii* has been the source of an array of cultivars. Usually purplish to sometimes white, pinkish, or nearly red, fragrant flowers typically with straight corollas having orange in the throats allow quick recognition of this species.

Our other member of sect. NEEMDA, *Buddleja Lindleyana,* is cultivated and naturalized beyond its homeland in China and nearby parts of eastern Asia. Although less hardy than the preceding species, *B. Lindleyana* seems to be better established in our area. It is present in and out of cultivation in probably all of the Southeastern States and Texas, being most clearly "naturalized" from North Carolina to southern Florida. Escaped populations arise on disturbed ground, roadsides, and shores and in pine woods. This species differs most saliently from *B. Davidii* in having longer, curved corolla tubes more abundantly provided with glandular hairs, usually simple lateral dichasia, leaf margins entire to irregularly crenate or dentate, or infrequently unevenly serrate (vs. generally distinctly serrate), no stipules (ephemeral in *B. Davidii*), and polygonal (vs. linear-fusiform) seeds.

Sect. NICODEMIA (Ten.) Leeuw. is represented by *Buddleja madagascariensis* Lam., $2n = 38$, an attractive garden species from Madagascar that escapes to disturbed sites in central-western peninsular Florida. Its yellowish or somewhat orange corollas with the stamens inserted high in the tube (vs. near or below the middle), tetralocular (vs. bilocular) ovaries, and berries (vs. capsules) are unique among our species. (I have not seen fruiting material from the United States.) Dried specimens are densely brownish-tawny pubescent. *Buddleja madagascariensis* flowers in the Southeast during winter, as opposed to the summer or autumn blooming of the two other species.

The foremost taxonomic treatments of *Buddleja* have been by Bentham (1846, the entire genus), Marquand (species in the Old World), Leeuwenberg (1979, African and Asian species), Norman (1967, 1982, species from North America and Ecuador), and Norman & Smith (in Smith *et al.,* 1976, species from Santa Catarina, Brazil). Divergent views complicate the infrageneric taxonomy. Bentham recognized two sections subdivided into components of unstated rank; Marquand rejected Bentham's arrangement and set up four "convenient" series for species in the Old World. In 1979 Leeuwenberg explained in effect that Marquand's series depend on few or single and feeble characters and consequently incorporated them all in his large, emended, and not subdivided section NEEMDA. Leeuwenberg correctly changed the name of Bentham's sect. *Lozada* to sect. BUDDLEJA, restricting it to three American species.

Leeuwenberg's two other sections are based on former genera from the Old World. The three species of sect. CHILIANTHUS (Burchell) Leeuw. stand out in *Buddleja* because their stamens are exserted on long filaments from broad and shallow corolla tubes. Chromosomal morphology and number help bind this section to the rest of the genus. Members of Leeuwenberg's sect. NICODEMIA have berries, rather than the capsules that are more typical of other species of the genus. The merger of *Nicodemia* with *Buddleja* into one genus is supported by hybridization, anatomy, limited chemical data, chromosomal morphology, and chromosome numbers (Leenhouts, 1962; Moore, 1947, 1960).

Norman will revise the infrageneric taxonomy in her upcoming treatment of the South American species.

Buddleja is probably most closely related to *Emorya,* from the New World, and *Nuxia,* from the Old, according to Leeuwenberg (1979) and Norman (1967). In contrast with *Buddleja, Emorya* has leaves with sinuate margins (unusual

in *Buddleja*), stamens exserted on long filaments from long corolla tubes (vs. on short filaments from long corolla tubes and usually included, or exserted on long filaments from short corolla tubes), styles protruding beyond the anthers, and a glabrous annular disk at the base of the ovary. Attempted crosses between *Emorya* and *Buddleja* have so far failed, despite the near morphological identity of their chromosomes.

Nuxia has relatively short corolla tubes bearing exserted stamens on filaments longer than those in most species of *Buddleja*. Section CHILIANTHUS has been included in and approaches *Nuxia* in having similar flowers and pollen (Punt, 1980; Punt & Leenhouts) and in the distribution of iridoids (Hegnauer & Kooiman). *Nuxia* is distinguished from sect. CHILIANTHUS and from the rest of *Buddleja*, however, by apically confluent (vs. separate) anther cells.

Nuxia, Emorya, and *Buddleja* sensu lato have the base chromosome number 19 in common.

Norman (1967, 1982), Ariza Espinar, and Norman & Smith (in Smith *et al.*) showed over thirty American species to be dioecious, usually fairly obscurely so. Staminate and carpellate flowers were similar externally or infrequently differed in size and/or shape; young sterile ovaries were either stunted or similar to fertile ones; and infertile anthers were reduced. Ariza Espinar told of conspecific staminate and carpellate buddlejas being described as separate species. Norman (1982) discovered *Buddleja Jamesonii* Bentham and *B. americana* to be trioecious (perfect, carpellate, and staminate flowers in different collections). One otherwise staminate plant of *B. racemosa* Torrey bore a few seeds, and carpellate plants of the same species in cultivation formed a small number of viable seeds, seemingly without pollination. This may have been due either to apomixis or to incompletely sterile anthers (Norman, 1967). If Ariza Espinar's suspicions are borne out, three species in Argentina have functionally perfect flowers, and Norman (pers. comm.) reports perfect flowers in at least the South American *B. tubiflora* Bentham and *B. australis* Vell.

Species from the Old World are less well studied in this regard. In *Buddleja Davidii* and *B. Lindleyana* only a portion of the flowers set fruit, frequently with inflorescences devoted completely or nearly so to either flowers that set fruit or presumably staminate ones that wither without forming capsules. (In 1984 almost all of the flowers of an individual of *B. Davidii* collected wild and grown in the Arnold Arboretum produced fruits. The pollen probably came from several nearby members of the same species.) Moore (1967) related the production of viable vs. nonviable pollen in the Asian species *B. crispa* Bentham cultivated in Canada to the season (i.e., under photoperiodic control?).

Certain species of *Buddleja* are self-compatible; others (including *B. Davidii*) are self-incompatible or nearly so (Keenan, 1969a; Moore, 1949, 1952).

Buddlejas usually grow completely in the open, or in scrubby woods or at their edges, and they commonly occur in disturbed or rocky places, at high elevations, on bluffs or steep slopes, and in dry (to wet) soil. *Buddleja Davidii* and other species tolerate high concentrations of calcium.

Flowers of *Buddleja Davidii* are sufficiently alluring to butterflies and other insects to serve as popular study sites for lepidopterists and as textbook examples of flowers visited by butterflies.

Diploid ($2n = 38$) species of *Buddleja* grow in Asia, Africa, and America. Numerous tetraploids are present in Asia and America, and probably also on Madagascar and nearby islands. One hexaploid is known from the New World (Norman, pers. comm.), while in Asia there are several hexaploids, as well as two known 12-ploids and one mixed 8-, 16-, and 24-ploid species.

Among species from the Old World cultivated in Ottawa, Canada, Moore (1961) found most polyploids to be long-day plants (or to flower late in the season by virtue of requiring a preliminary period of growth) and to have spicate inflorescences. He interpreted both features as evolutionary advancements over the short-day requirement and the often shorter, leafier, and otherwise presumably less-specialized inflorescences of most diploid species. (Norman, 1967, disagreed about evolutionary trends in the inflorescences.) Moore (1961) supposed multiple diploid species to have been ancestral to the Asian polyploids, which he held to have "spread little beyond the point of origin" (p. 278). They are clustered in the Asian area of high species concentration mentioned above (see also Janaki Ammal). Their mutual inclination toward the long-day photoperiod notwithstanding, the polyploids are not the northernmost species.

As envisioned by Moore (1961), the relatively primitive diploid buddlejas crossed the formerly narrower Atlantic Ocean to the New World under equatorial short-day conditions and radiated northward secondarily. This accords with Norman's (1967) hypothesis that the North American species arose from South American ancestors, since the former are most similar to and have morphological "prototypes" among those in South America. (For the opposite view that *Buddleja* spread from North to South America, see Raven & Axelrod.)

In 1967 Moore observed that the New and Old World buddlejas "differ greatly," and he (1960) was unable to cross members of one group with those of the other. (At least two New World–Old World hybrids have been reported; one of these is probably a backcross involving gametes differing in chromosome number.) Moore and other authors have hybridized even morphologically dissimilar Old World species, and apparent hybridization among American species occurs repeatedly (see comments under individual species in Norman, 1967, 1982). All three of our introduced species are thought to be parents of various hybrids. Artificial crosses in *Buddleja* range in outcome from reduced fertility to early developmental failure of the F_1 hybrids.

Species of *Buddleja* are most important to humans as ornamentals and as medicinal plants. All three species in our area were certainly introduced for their decorative value, which they share with several other species, as well as with various hybrids and cultivars. Applications in folk medicine counter a wide variety of ills in both hemispheres. Houghton (see also Bisset, 1980a, 1980b) compiled a survey of medicinal uses focused on eight species and attempted to relate attributed benefits to chemical constituents: remedies for the skin and eyes possibly relate to flavonoids, aucubin (an iridoid), and saponins; respiratory treatments may be based on terpenes or saponins; antiseptic qualities could be related to the aglycone from aucubin; diuresis might result from aucubin or flavonoids; and sedative and analgesic properties are possibly due to alkaloids, although scattered reports of alkaloids in *Buddleja* remain

inadequately substantiated and have in some cases been contradicted. In an earlier study Houghton isolated lignans from *B. Davidii,* and in 1984 he cited other literature documenting lignans as antihepatotoxics. Singh and colleagues looked into hypotensive activity from *B. asiatica.* Some, if not all, species are poisonous to humans.

A small number of additional uses for species of *Buddleja* are noted in the literature. Buddledin sesquiterpenes (see Yoshida *et al.*), as well as saponins, help to account for utilization of *Buddleja* as fish poison. Wood from species of *Buddleja* has limited utility as fuel. *Buddleja americana* is burned as an incense in the New World (Morton), and at least one other species is used the same way during funeral ceremonies in China (S. Y. Hu, pers. comm.). Tree species yield wood used in construction. Flowers of *B. asiatica* have been cooked with meat and used in wine (Leenhouts, 1962); those from *B. marrubiifolia* Bentham have given color to Mexican foods; and "a substitute for saffron" comes from flowers of *B. utilis* Kränzlin (Macbride).

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THE MONTANE VEGETATION AND FLORA OF MARGARITA ISLAND, VENEZUELA

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The island of Margarita (11°N, 64°W) is physically and politically a part of Venezuela, constituting most of the state of Nueva Esparta, which also includes the two much smaller islands of Coche and Cubagua. The three islands lie on the continental shelf to the north of the peninsula of Araya, and Margarita is separated from the mainland by a channel approximately 25 km wide. Margarita is the most extensive and mountainous of the Venezuelan islands and is the only one to support moist evergreen montane vegetation.

The montane vegetation of Margarita has particular ecological interest because of its exceptionally low altitude and its apparent reliance on frequent and regular nocturnal cloud cover for the maintenance of moist conditions—features that are shared by only two other localities (the Serranía de Macuira, on the Guajira peninsula, Colombia; and Cerro Santa Ana, on the Paraguaná peninsula, Venezuela) on the Caribbean coast of South America (Sugden, 1982a, 1982b, 1983). Some factors that have been suggested as determinants of the peculiar physiognomy of montane rain forests at higher altitudes—for instance, low temperature and low insolation due to diurnal cloud cover (Leigh, 1975; Grubb, 1977)—are apparently unimportant in the Margarita mountains, while others such as wind have greater significance, as will be shown in this article.

The montane forests of Margarita are also of phytogeographic interest due to their insularity and their location between the South American mainland and the arc of the Lesser Antilles. Johnston (1909) collected about 165 species of vascular plants in the mountains, eight of which were apparently endemic. Subsequent collecting has increased the total number of montane species to at least 220, while the number of endemics (due to further collections from elsewhere) has dwindled to four or five dubious ones. It has been shown by Ortega (1982) and Sugden (1983) (for the pteridophyte and woody floras, respectively) that most of the montane species are quite widely distributed in the Neotropics; not surprisingly, the affinities with the mainland are stronger than those with the Lesser Antilles. I have presented evidence to suggest that the montane vegetation of Margarita is of recent origin (probably less than 10,000 years B.P.), and that the flora owes its present character and composition to random events of long-distance dispersal and establishment (Sugden, 1983).

The first account of the montane vegetation of Margarita was written by Johnston (1909). He recorded dense evergreen woods above 300 m, which

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became increasingly stunted and laden with epiphytes at higher altitudes. He described the top of the mountain, covered on the sheltered side with crooked trees, their branches thick with moss and dripping with moisture, and on the windward side by low shrubs and large bromeliads. This vegetation contrasted strongly with that of the lowlands, which—like most of the Caribbean lowlands of South America—supported dry deciduous woodlands and thorn and cactus scrub. This contrast also attracted the attention of Alexander (1958), who (like Johnston) considered that regular cloud cover above 400 m was responsible for the difference. He further suggested that the extremely stunted vegetation close to the highest ridges and summits owed its character to persistent high winds.

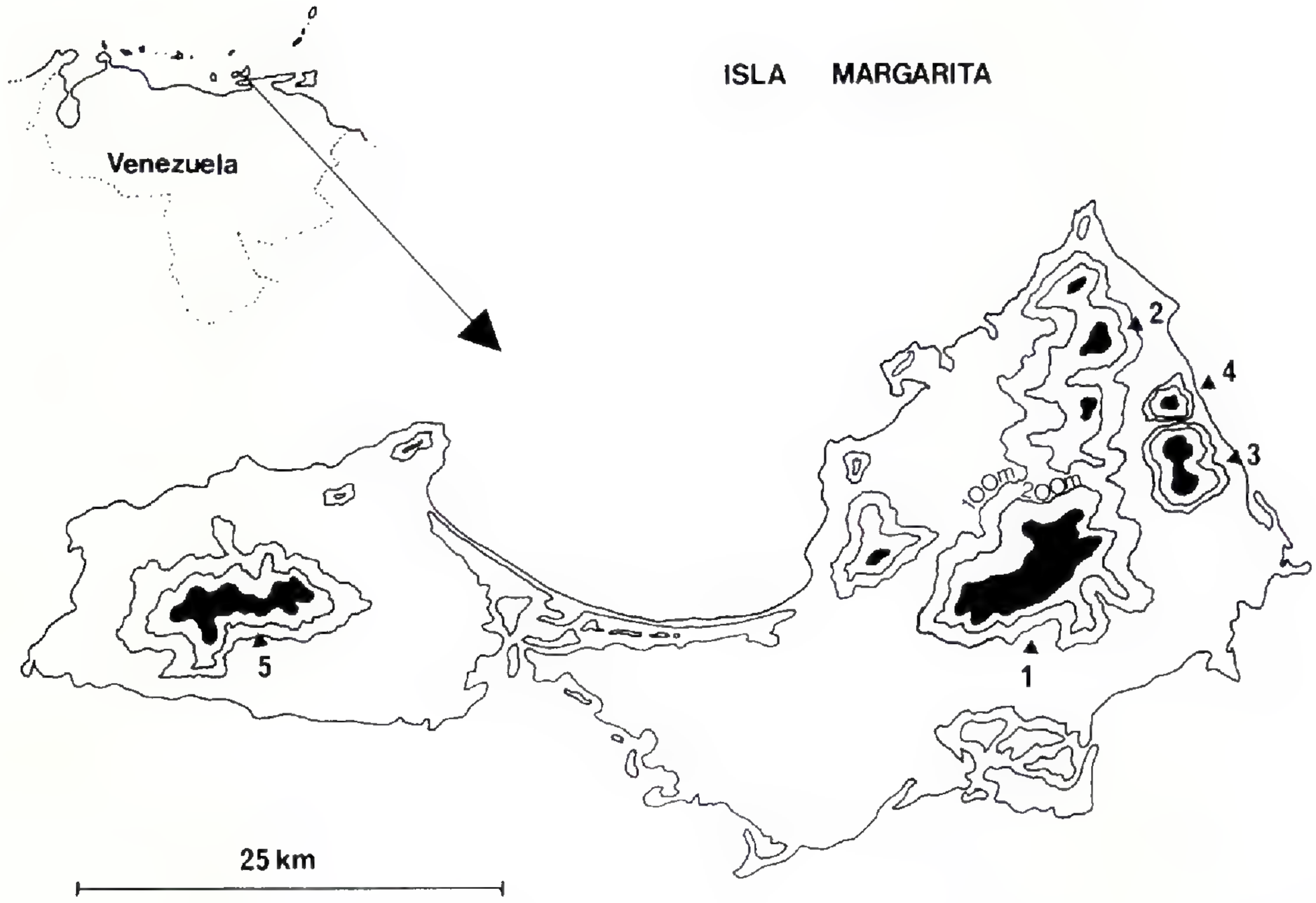
Ortega (1982) divided the upland vegetation into the categories of *selva pluvial intermedia* (intermediate rain forest), *selva nublada* (cloud forest), *bosque enano* (dwarf forest), and *bosque degredado en forma de páramo* (degraded forest in the form of páramo), the last of these occurring on the highest wind-swept slopes of Cerro Copey (930 m), the main massif of the island. I included all these types together under the general term of upper montane rain forest (Sugden, 1983).

All of these descriptions and classifications were included as brief adjuncts to floristic, geographic, and phytogeographic accounts and analyses. The purpose of the present account is to provide a more comprehensive and definitive description of the montane vegetation, which will serve as a basic source of information and also as an introductory framework for other analyses of physiognomy, regeneration, leaf anatomy (Sugden, 1985), and tree architecture in the Margarita mountains. Good descriptions of the dry vegetation on the lower slopes and plains of Margarita have been given by Johnston (1909), Marcuzzi (1950), and Alexander (1958).

GEOGRAPHY AND GEOLOGY

Margarita has the shape of an irregular dumbbell (see MAP 1), with two mountainous extremities connected by a low-lying isthmus, much of which consists of the mangrove swamps of La Restinga. The mountains of the eastern part of the island (Paraguachoa) comprise a central massif rising to 930 m with several smaller outliers to the north and east. The main ridge, the Serranía del Copey, runs in a northeast–southwest arc, with its highest point variously known as Cerro San Juan, Cerro Grande, or Cerro Copey (Jam, 1962); in the present account the last of these names is used. A steep-sided valley separates the northern end of the ridge from Cerro Tragaplata (also known as Cerro Chico), a broad dome 700 m high. On the eastern coast, separated from the main ridge by the plain of La Asunción, stand a pair of outlying mountains, the saddle-shaped Cerro Matasiete (660 m) and the pyramidal Cerro Guayamurí (490 m).

These four mountains, Copey, Tragaplata, Matasiete, and Guayamurí, support all of the undisturbed montane vegetation of eastern Margarita. Geologically, they are very similar to one another; the upper slopes (above ca. 350



MAP 1. Margarita Island, showing principal localities mentioned. Areas above 400 m marked in black. 1 = Cerro Copey, 2 = Cerro Tragaplata, 3 = Cerro Matasiete, 4 = Cerro Guayamurí, 5 = Macanao.

m) consist of peridotite, an ultramafic igneous rock, which in places is serpentinized (Jam & Mendez-Arocha, 1962; Y. Chevalier, pers. comm.).

The mountains of Macanao (the western part of the island) attain a maximum elevation of 780 m and form a single rugged ridge with three principal peaks. The highest of these, Cerro Los Cedros, is a sharp peak supporting a small patch of evergreen forest on the windward side of its summit. The entire range of Macanao consists of metamorphic schists and gneisses (González de Juana & Vignali, 1972).

CLIMATE

At 11°N latitude, Margarita is subject to strong east–northeasterly trade winds for almost the entire year and also lies within the anomalous region known as the South Caribbean Dry Zone (Lahey, 1958), where mean annual precipitation is always less than 1000 mm and often less than 500 mm. The climate of Margarita becomes increasingly wet with higher altitude and with greater proximity to the eastern (windward) coast (Contreras, 1967). In the eastern lowlands there are two short rainy seasons, in December–January and July–August, while in Macanao there is only one, in July–August (see FIGURE 1); mean annual precipitation in the two areas is ca. 550 mm and 300 mm, respectively. The total annual rainfall varies considerably at both ends of the island, ranging from 96 to 1532 mm over 20 years at La Asunción (Alexander, 1958), and from 138 to 720 mm over 12 years at Boca del Pozo (data from information

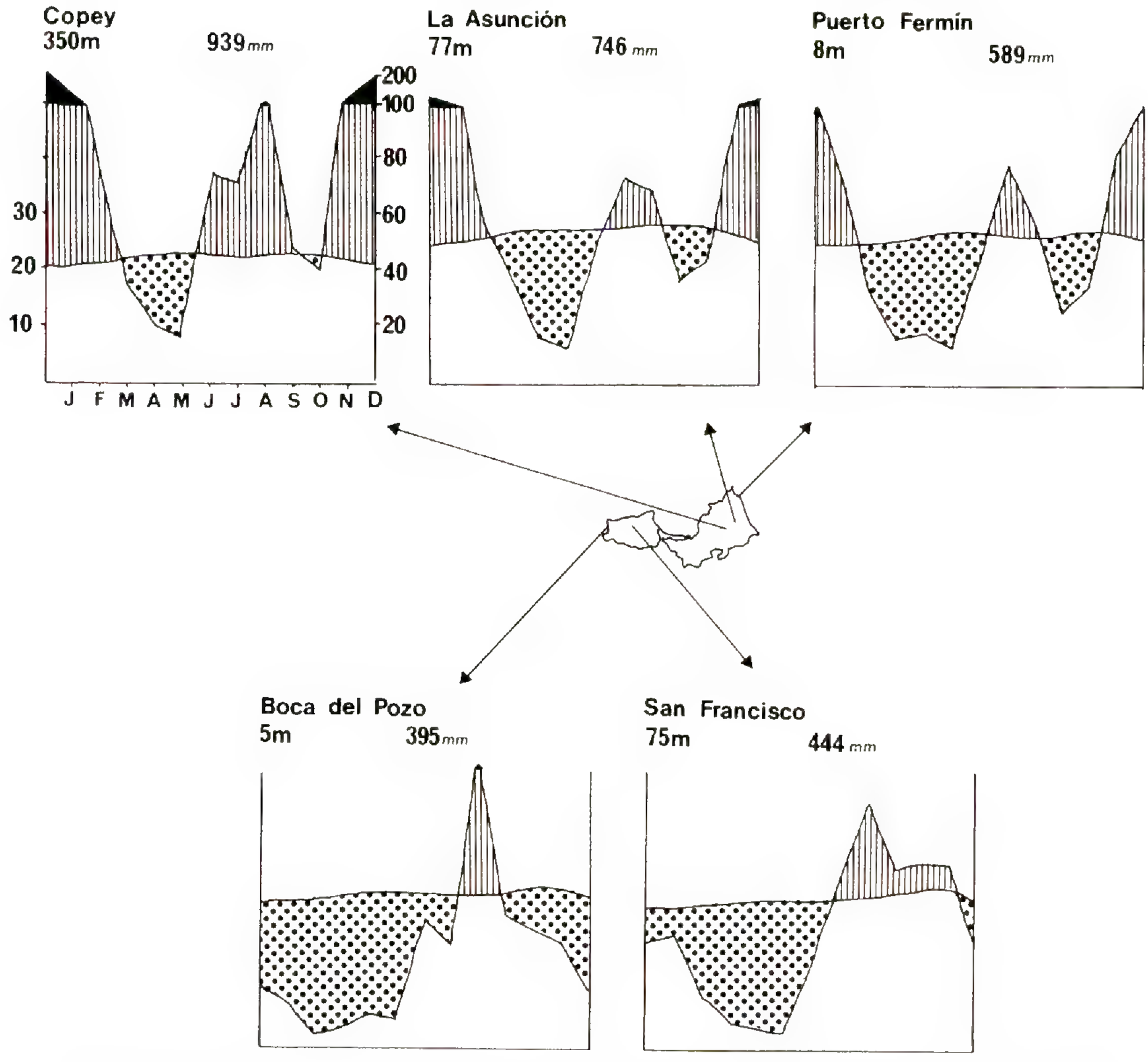


FIGURE 1. Climatic diagrams for Margarita Island (localities as in MAP 1). Left scale, mean monthly temperature (°C); right scale, mean monthly precipitation (mm); altitude and mean annual precipitation also shown. Data covering most years from 1953 to 1981, taken from information kindly supplied by Ministerio del Ambiente y de los Recursos Naturales Renovables (MARNR), Caracas. Diagrams show increase in precipitation with altitude at eastern end of island, increased aridity at western end.

kindly supplied by the Ministerio del Ambiente y de los Recursos Naturales Renovables, Porlamar).

The increase in precipitation with altitude is not known, since there are no climatic stations above 400 m. The highest station, at 350 m on the eastern slopes of Cerro Copey, has recorded a mean annual precipitation of ca. 950 mm, with a range of 222 to ca. 1900 mm since 1951.

Precipitation at higher altitudes is certainly greater, due to cloud droplet interception by the vegetation. On most nights throughout the year, the eastern mountains are capped with orographic clouds, which generally descend late in the afternoon and lift during mid-morning. On 271 days between September, 1982, and September, 1983, I recorded the times of day when clouds descended and lifted on Cerros Copey, Matasiete, Tragaplata, and Guayamurí and made notes on the approximate altitude of the cloud base at dusk on each mountain.

The observations were made from suitable vantage points in the lowlands and during the course of routine fieldwork on Cerro Copey. On only seven occasions were clouds absent from the peaks for more than 48 hours; there were no periods of more than 72 hours without cloud cover. During the same year, there was one interval of ten days when the clouds never lifted from the summits even at midday. The cloud base is generally lower on the windward sides of the mountains. Thus, on Cerros Guayamurí, Matasiete, and Tragaplata, the clouds descend to ca. 350 m on the eastern slopes and to 400–500 m on the western. On Cerro Copey, which is farther inland, the lower limits on the windward and leeward slopes are ca. 450 m and 550 m, respectively.

No systematic records have been made of cloud cover on the mountains of Macanao, but limited observations suggest that it is far less regular (Alexander, 1958); cloud-free periods of up to several weeks may be common. The cloud base appears to be at about 600 m. According to Alexander, the Macanao mountains receive less cloud cover because they are aligned more or less parallel to the prevailing wind; the eastern mountains present a more perpendicular face to the wind, forcing the air to rise rather than to pass on either side. A further cause for reduced cloud cover on Macanao may be a warming of the airstream as it passes over the island from east to west; this could cause a generally higher cloud base in the west.

The extent to which cloud-droplet interception contributes to the total precipitation on the mountains is unknown. Generally the vegetation on the upper slopes of Cerro Copey is dripping with moisture after the clouds have lifted in the morning, although there is relatively little surface moisture even on the understory leaves and branches by late afternoon. The soil surface is never dry to the touch, and on the highest windswept slopes of Cerro Copey it is generally wet and slippery. Streams flow only after rain, which fell heavily on 27 days and lightly or intermittently on an additional 34 during my 271 days of observation. Whatever the total precipitation, however, it is reasonably certain that cloud cover on these mountains increases humidity and offsets the highly seasonal rainfall regime; the probability of periodic drought decreases dramatically with increasing altitude.

A steep temperature gradient, 0.97°C/100 m altitude increase, has been recorded on Cerro Copey by Drs. C. Schubert and E. Medina (pers. comm.) using soil probes at depths of 30–40 cm. The mean annual temperature at the summit, recorded in this way, was approximately 19°C. Monthly and daily maximum and minimum temperatures have not been recorded in the mountains; in a maritime, low-altitude situation of this kind, however, strong variation and extremes of heat and cold would not be expected.

The strength of the wind increases with altitude, and at the summit of Cerro Copey there is an almost perpetual gale. There are no extensive data on wind speed on the mountain, but according to the technicians at the summit telecommunications station, gusts of more than 80 km per hour have been recorded by their anemometer. The direction of the wind varies little during the year. I have observed light southerly or southwesterly winds on infrequent occasions during the July–August rainy seasons. Otherwise, the flow of the trade winds is interrupted only by the passage of hurricanes and tropical storms within 150

FIGURE 2. Cerro Matasiete, showing contrasting dry vegetation (lower slopes) and evergreen vegetation (upper slopes).

km of the island, which has occurred seven and nine times, respectively, during the last century (Alexander & Bertness, 1982).

UPLAND VEGETATION

METHODS

Fieldwork was carried out in August, 1981, January, 1982, and September, 1982–September, 1983. The greater part of the work was carried out on Cerro Copey, which has a road to its summit and therefore has easily accessible vegetation; this vegetation is mostly undisturbed. Occasional ascents were also made on foot to the summits of Matasiete (twice), Guayamurí (once), Tragaplata (once), and the mountains of Macanao (twice).

Herbarium collections and floristic notes were made during the course of regular visits (every two to three weeks) to a dozen sites between 400 m alt. and the summit of Cerro Copey, and particular efforts were made to ensure that fertile specimens were eventually collected from unfamiliar plants initially encountered in the vegetative condition. Collections and notes were also made routinely during the trips up and down the summit road, occasional forays into other parts of Cerro Copey, and the ascents of the other mountains. I have checked and supplemented the floristic information thus obtained by reference to the excellent collections from Isla Margarita in the herbarium of the Sociedad de Ciencias Naturales La Salle, in Caracas, and to Johnston's flora (1909) and some of his duplicates at Kew. A previous list of the woody plants of the eastern mountains of Margarita (Sugden, 1983) requires some revision and updating in light of the recent fieldwork.

The principal criteria for distinguishing vegetation types in the upland zone included height of canopy, diameter of boles, and presence and levels of abundance of various habits, life-forms, major taxa (deciduous trees, bryophytes, vascular epiphytes, woody lianas, palms, understory shrubs, herbs), and (in some cases) individual species. Except for easily quantifiable characters such as bole diameter, these observations were mainly qualitative but nevertheless detailed. Quantitative characterizations of leaf anatomy in the major vegetation types, and of floristics and physiognomy in one of them, are the subjects of separate articles (Sugden, 1985; Sugden, in preparation).

Soils were sampled at ten sites between 400 and 900 m alt. on Cerro Copey. At each site a pit was dug to a depth of ca. 50 cm in order to assess physical characteristics; supplementary information was also obtained from road cuts nearby. Samples for chemical analysis were taken from the top 5 cm and from the upper mineral layer (10–30 cm), the exact depth depending on the site. Analyses were carried out by the Centro de Ecología, IVIC, Caracas (details of standard procedures available on request).

Results

General Remarks

The ecotone between the predominantly deciduous vegetation of the lower slopes and the mostly evergreen upland vegetation is generally well defined (Figure 2) and is particularly obvious during the long dry seasons. More often than not, it is marked by the appearance of large trees of *Clusia rosea* with wide, spreading crowns and also by the appearance of an epiphytic and herbaceous flora that becomes increasingly diverse with higher altitude. Although a few deciduous tree species are present above the ecotone, for convenience I shall use the term "evergreen upland vegetation" to embrace all the physiognomic types found above this level.

The precise level of this ecotone corresponds closely to the level of the cloud base on each mountain. Thus, evergreen upland vegetation begins at ca. 350 m alt. on the windward slopes and ca. 450 m alt. on the leeward slopes of Cerros Guayamurí, Matasiete, and Tragaplata, and at ca. 400 m alt. on the windward side and 500–550 m alt. on the leeward side of Cerro Copey. On all four mountains thin ribbons (often less than 30 m wide) of "gallery forest" extend downward along the deeper gullies with permanent groundwater, occasionally to as low as 100 m above sea level; these are especially well developed on Cerro Copey.

The evergreen upland vegetation can be divided into four quite distinct physiognomic types, which can be further subdivided according to physiognomic and/or floristic criteria into a total of ten subtypes:

1. Transition Forest
   a. with *Clusia rosea*
   b. without *Clusia rosea*
2. Cloud Forest
   a. tall

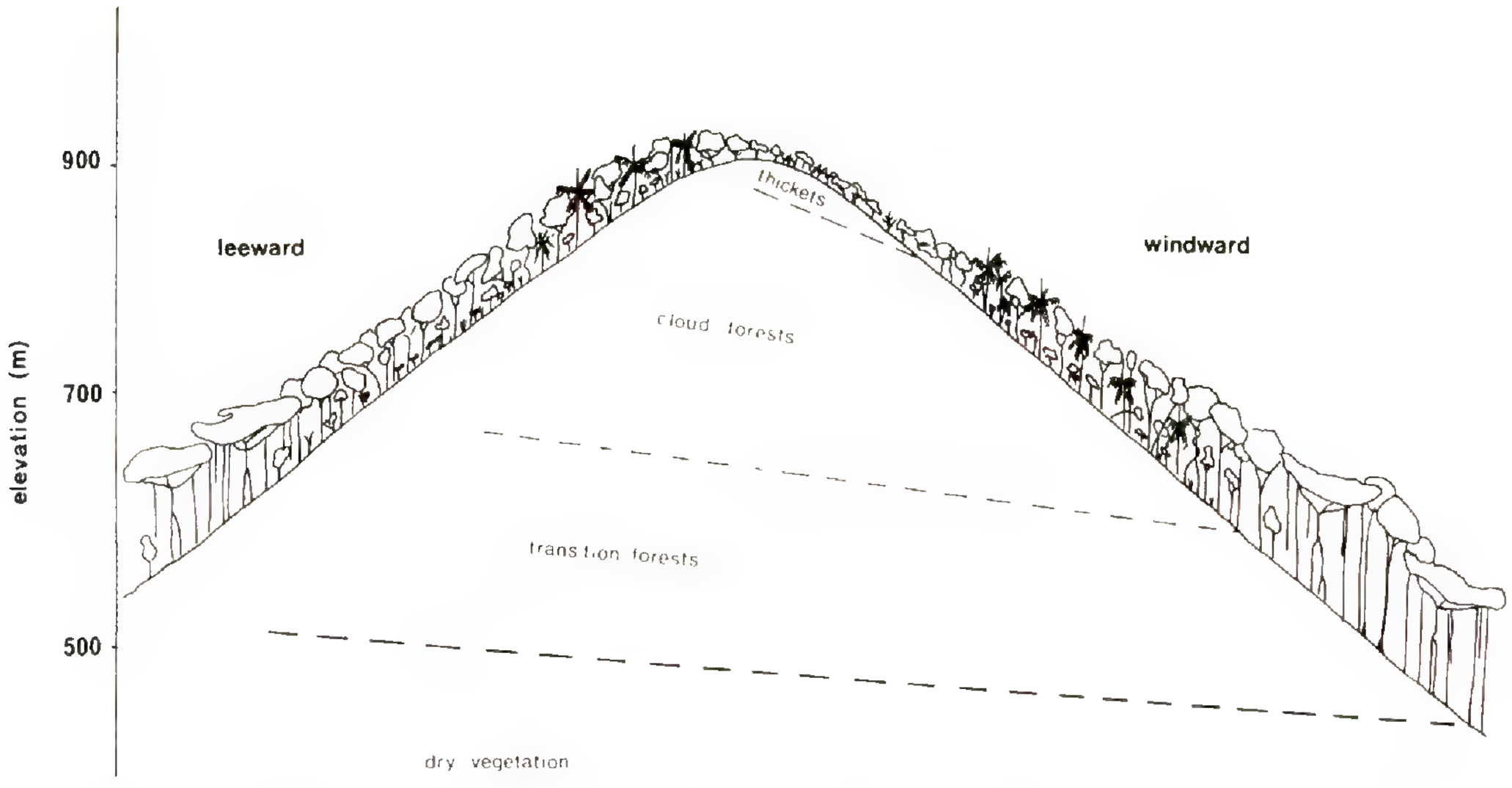


FIGURE 3. Idealized profile of Cerro Copey, showing distribution of vegetation types. (Trees not drawn to scale.)

b. pole
c. lower palm
d. upper palm

3. Wet Thicket
   a. tall woody
   b. short woody
   c. herbaceous
4. Grassland

The descriptions that follow are of the upland vegetation of Cerro Copey, where the distinctions between the various vegetation types and subtypes are best developed; as the highest and most extensive mountain on the island, Cerro Copey has the greatest physiognomic and floristic diversity. Cerros Guayamurí, Matasiete, and Tragaplata, and the mountains of Macanao, are considered briefly in a subsequent section.

The flowering plants of Cerro Copey, and their distributions in the vegetation types, are listed in TABLE 1. My observations of the fern flora are not sufficiently detailed to justify similar treatment. A complete list of the pteridophytes of Margarita, almost all of which occur on Cerro Copey, has been compiled by Ortega (1982), and some of these species will be mentioned in the descriptions that follow. TABLE 2 provides an outline of the principal chemical features of the soils in each of the four major vegetation types. The principal physiognomic differences between these types are summarized in TABLE 3. An idealized profile of the vegetation is shown in FIGURE 3.

Types of Vegetation

1. TRANSITION FOREST. The term "transition forest" is analogous to the *selva de transición* of Steyermark and Huber (1978), used to denote the forests

intermediate between the savannas and cloud forests on the slopes of the Venezuelan Cordillera de la Costa, near Caracas. On Cerro Copey Transition Forest is the first mainly evergreen vegetation type encountered on the ascent. It occupies an altitudinal band of 150–200 m and reaches a maximum elevation of ca. 700 m on the leeward slopes. It is distinguished from the forests at higher altitudes by its relatively low number of vascular epiphytes and bryophytes and its comparatively high frequency of woody lianas and individuals of deciduous tree species. Transition Forest has the widest leaf-size spectrum (for canopy trees) of any of the major vegetation types, from the leptophylls of *Calliandra panlosia* to the mesophylls of *Croton xanthochloros* (Sugden, 1985).

Soils in the Transition Forest are normally up to 80 cm (rarely more than 100 cm) deep. There is a thin layer of dryish litter, covering a humus layer 1–5 cm thick that contains abundant roots. The mineral horizons are clayey, but with a distinct crumb structure, and yellowish brown. These soils have the highest pH (6.25–6.85) of any of the upland ones and also have a very high magnesium content (see TABLE 2).

There are two subtypes of Transition Forest:

a. **With Clusia rosea.** Located on the more sheltered slopes of Cerro Copey, Transition Forest with *Clusia rosea* (FIGURE 4) is the tallest vegetation on Margarita, reaching heights of up to 30 m; in windier places the canopy is considerably lower (15–20 m). The characteristic architecture of *C. rosea* (with spreading plagiotropic branches overlapping to produce an imbricate effect), together with its very dark foliage, enables ready identification from a distance; indeed, *C. rosea* is the only species that is readily distinguishable in aerial photographs of the island. From within the forest, *C. rosea* can be recognized by its masses of thick, usually pale gray, conspicuously lenticellate aerial roots. Other large trees prominent in this vegetation are *Croton xanthochloros, Terminalia amazonia,* and *Ficus nymphaeifolia,* all deciduous and with a leafless period of less than one month. *Ficus nymphaeifolia,* like *C. rosea,* is a "strangling" hemiepiphyte. In this vegetation, as in all the types subsequently described, the canopy is quite closed and uniform, without "emergent" trees.

The lower strata under *Clusia rosea,* which is the sole canopy species in much of the forest, are generally poorly developed. The understory is open and free of obstacles. Herbaceous species are rare, and shrubs are virtually absent. Woody lianas are more frequent, and a *Philodendron* sp. is a common herbaceous climber.

b. **Without Clusia rosea.** This forest subtype is more heterogeneous than the previous one. It occurs over a similar range of altitudes, and its chief features, apart from the rarity of *Clusea rosea,* are a higher diversity of tree species and a somewhat lower (10–15 m) canopy. Many of the common Cloud Forest species (see below) occur here; *Guapira* cf. *fragrans, Daphnopsis americana, Maytenus karstenii, Myrcia* cf. *coriacea,* and *Roupala montana* are especially prominent. Important deciduous species are *Calliandra panlosia, Croton xanthochloros, Tabebuia chrysantha,* and *Terminalia amazonia.* Few tree species are confined to this zone; those that are common here and rare on other parts of the mountain include *Calliandra panlosia* and *Linociera caribaea.*

TABLE 1. **The distribution of flowering-plant species in the montane vegetation types of Cerro Copey.**

		TRANSITION FOREST		CLOUD FOREST				WET THICKET			
		with *Clusia rosea*	without *Clusia rosea*	Tall	Pole	Lower palm	Upper palm	Tall woody	Short woody	Herbaceous	GRASS-LAND
WOODY CANOPY PLANTS											
Aquifoliaceae	*Ilex guianensis* (Aublet) Kuntze	–	–	+	+	+	+	+	+	–	–
Araliaceae	*Dendropanax arboreum* (L.) Decne. & Planchon	–	–	+	+	+	+	–	–	–	–
	Oreopanax capitatum (Jacq.) Decne. & Planchon	–	–	+	+	+	–	–	–	–	–
Bignoniaceae	*Tabebuia* cf. *chrysantha* Nicholson	+	+	+	+	+	+	+	+	–	–
Bombacaceae	*Ceiba pentandra* (L.) Gaertner	+	+	–	–	–	–	–	–	–	–
Boraginaceae	*Cordia* cf. *hirta* I. M. Johnston	–	+	+	+	–	–	–	–	–	–
	Cordia polycephala (Lam.) I. M. Johnston	–	–	–	–	–	–	–	+	–	–
Burseraceae	*Protium* cf. *tenuifolium* (Engler) Engler	+	+	+	+	–	–	–	–	–	–
Celastraceae	*Maytenus* cf. *karstenii* (Klotzsch) Reissek	+	+	+	+	+	+	+	+	–	–
Chrysobalanaceae	*Licania membranacea* Sagot ex Laes.	–	–	+	+	+	–	–	–	–	–

Clusiaceae	Clusia cf. flava Jacq.	–	–	–	–	+	+	++	+	(+)	–
	Clusia cf. myriandra (Bentham) Planchon & Trelease	–	–	–	–	–	–	+	+	–	–
	Clusia rosea Jacq.	+	(+)	(+)	(+)	(+)	(+)	–	–	–	–
Combretaceae	Terminalia amazonia (Gmelin) Exell	+	+	+	+	+	+	–	–	–	–
Compositae	Sp. indet. (Mutisieae)	–	+	–	–	–	–	+	–	–	–
Erythroxylaceae	Erythroxylum densum Rusby	–	–	–	–	–	–	+	+	(+)	–
Euphorbiaceae	Croton xanthochloros Croizat	+	+	+	+	(+)	(+)	–	–	–	–
	Margaritaria nobilis L.f.	–	+	+	+	+	+	(+)	–	–	–
Flacourtiaceae	Casearia cf. decandra Jacq.	?	?	+	–	–	–	–	–	–	–
	Casearia guianensis (Aublet) Urban	+	+	(+)	–	–	–	–	–	–	–
	Casearia zizyphoides H.B.K.	(+)	+	–	–	–	–	–	–	–	–
	Sp. indet.	–	+	+	–	–	–	–	–	–	–
Lauraceae	Ocotea leucoxylon (Sw.) Mez	–	–	+	+	+	+	+	+	(+)	–
	Persea caerulea (Ruiz & Pavon) Mez	–	–	+	+	+	(+)	–	–	–	–
Leguminosae	Calliandra panlosia J.R. Johnston	+	++	+	+	–	–	–	–	–	–
	Cassia fruticosa Miller	–	(+)	(+)	(+)	(+)	(+)	(+)	+	–	–
	Inga macrantha J.R. Johnston	–	–	+	+	+	+	+	+	–	–
Marcgraviaceae	Ruyschia tremadena (Ernst) Lundell	–	–	–	–	–	–	–	+	(+)	–
Melastomataceae	Blakea monticola J.R. Johnston	–	–	+	+	+	+	+	+	–	–

TABLE 1 (*continued*).

		TRANSITION FOREST		CLOUD FOREST				WET THICKET			
		with *Clusia rosea*	without *Clusia rosea*	Tall	Pole	Lower palm	Upper palm	Tall woody	Short woody	Herbaceous	GRASS-LAND
	Clidemia hirta (L.) D. Don	–	–	–	–	–	–	(+)	+	(+)	–
	Miconia prasina (Sw.) DC.	–	–	+	+	–	–	–	–	–	–
Moraceae	*Ficus nymphaeifolia* Miller	+	+	+	+	–	–	–	–	–	–
	Ficus yoponensis Desv.	–	(+)	–	–	–	–	–	–	–	–
Myrsinaceae	*Rapanea guianensis* Aublet	(+)	+	+	+	+	+	+	+	–	–
Myrtaceae	*Marlieriopsis eggersii* Kiaerskou	–	–	+	+	+	+	+	–	–	–
	Myrcia cf. *coriacea* (Vahl) DC.	+	+	+	+	+	+	+	+	–	–
	Myrciaria sp.	+	+	+	+	–	–	–	–	–	–
Nyctaginaceae	*Guapira* cf. *fragrans* (Dum.-Cours.) Little	+	+	+	+	+	+	+	+	(+)	–
	Pisonia aculeata L.	+	+	–	–	–	–	–	–	–	–
Ochnaceae	*Ouratea guildingii* (Planchon) Urban	+	+	–	–	–	–	–	–	–	–
	Ouratea pyrifolia (Griseb.) Engler	–	–	–	–	–	+	+	–	–	–
Olacaceae	*Schoepfia schreberi* Gmelin	(+)	+	–	–	–	–	–	–	–	–

	Ximenia americana L.	(+)	+	–	–	–	–	–	–	–	–
Oleaceae	Linociera caribaea (Jacq.) Knobl.	(+)	+	(+)	(+)	–	–	–	–	–	–
Opiliaceae	Agonandra brasiliensis Bentham & Hooker	(+)	+	–	–	–	–	–	–	–	–
Palmae	Acrocomia sclerocarpa Martius	–	+	–	–	–	–	–	–	–	–
	Bactris falcata J.R. Johnston	–	–	+	+	–	–	–	–	–	–
	Euterpe karsteniana Engel	–	–	+	+	+	+	–	–	–	–
Polygonaceae	Coccoloba cf. rugosa Desf.	–	–	+	+	–	–	–	–	–	–
	Coccoloba sp. 1	+	+	–	–	–	–	–	–	–	–
	Coccoloba sp. 2	+	+	–	–	–	–	–	–	–	–
Proteaceae	Roupala montana Aublet	+	+	+	+	+	+	+	+	+	(+)
Rubiaceae	Coutarea hexandra (Jacq.) K. Schum.	(+)	+	–	–	–	–	–	–	–	–
	Guettarda odorata (Jacq.) Lam.	(+)	+	+	+	–	–	–	–	–	–
	Guettarda scabra (L.) Vent.	+	+	+	+	+	+	+	–	–	–
Rutaceae	Amyris ignea Steyerm.	+	+	–	–	–	–	–	–	–	–
	Amyris simplicifolia H. Karsten	?	?	–	–	–	–	–	–	–	–
	Esenbeckia grandiflora Martius	–	–	+	+	+	–	–	–	–	–
	Esenbeckia pilocarpoides Kunth	–	+	–	–	–	–	–	–	–	–
Sapindaceae	Cupania americana L.	+	+	(+)	(+)	(+)	(+)	–	–	–	–
Styracaceae	Styrax glaber Sw.	–	–	+	+	+	+	–	–	–	–

TABLE 1 (*continued*).

		TRANSITION FOREST		CLOUD FOREST				WET THICKET			
		with *Clusia rosea*	without *Clusia rosea*	Tall	Pole	Lower palm	Upper palm	Tall woody	Short woody	Herbaceous	GRASS-LAND
Symplocaceae	*Symplocos martinicensis* Jacq.	–	–	+	+	+	+	+	+	–	–
Thymeleaceae	*Daphnopsis americana* (Miller) J.R. Johnston	(+)	+	+	+	+	+	+	(+)	–	–
Violaceae	*Rinorea lindeniana* (Tul.) Kuntze	+	+	+	+	(+)	–	–	–	–	–
WOODY UNDERSTORY PLANTS											
Begoniaceae	*Begonia glabra* Aublet	–	–	(+)	+	+	–	–	–	–	–
Boraginaceae	*Tournefortia hirsutissima* L.	–	–	+	+	+	+	–	–	–	–
	Tournefortia volubilis L.	–	–	+	+	+	–	–	–	–	–
Ericaceae	Cf. *Orthaea* sp.	–	–	–	–	–	–	–	+	–	–
Erythroxylaceae	*Erythroxylum hondense* H.B.K.	–	–	+	+	+	+	–	–	–	–
Euphorbiaceae	*Acalypha macrostachya* Jacq.	–	–	+	+	–	–	–	–	–	–
	Actinostemon concolor Muell. Arg.	(+)	+	–	–	–	–	–	–	–	–
	Croton margaritensis J.R. Johnston	–	–	–	–	–	+	+	+	–	–

Malpighiaceae	Bunchosia sp.	–	–	+	+	–	–	–	–	–	–
	Hiraea reclinata Jacq.	+	+	–	–	–	–	–	–	–	–
Melastomataceae	Miconia laevigata (L.) DC.	–	–	(+)	(+)	–	–	–	–	–	–
Palmae	Geonoma pinnatifrons Willd.	–	–	+	+	+	–	–	–	–	–
Piperaceae	Piper aequale Vahl	–	–	?	?	–	–	–	–	–	–
	Piper dilatatum L.C. Rich.	–	–	?	?	–	–	–	–	–	–
	Pothomorphe peltata (L.) Miq.	+	+	–	–	–	–	–	–	–	–
Rubiaceae	Chiococca alba (L.) Hitchc.	+	+	–	–	–	–	–	–	–	–
	Gonzalagunia spicata (Lam.) Gómez	–	+	+	+	(+)	–	–	–	–	–
	Psychotria barbiflora A. DC.	–	–	?	?	+	–	–	–	–	–
	Psychotria carthaginensis Jacq.	–	–	+	+	+	–	–	–	–	–
	Psychotria muscosa (Jacq.) Steyerm.	–	–	+	+	++	(+)	–	–	–	–
Solanaceae	Cestrum sp. 1	–	–	+	+	+	–	–	–	–	–
	Cestrum sp. 2	–	–	–	–	–	–	+	–	–	–
	Solanum arboreum Humb. & Bonpl. ex Dunal	–	–	+	–	–	–	–	–	–	–
	Solanum nudum Humb. & Bonpl. ex Dunal	–	–	+	+	+	(+)	–	–	–	–
Violaceae	Rinorea melanodonta Blake	+	+	+	+	+	(+)	–	–	–	–

TABLE 1 (*continued*).

		TRANSITION FOREST		CLOUD FOREST				WET THICKET			
		with *Clusia rosea*	without *Clusia rosea*	Tall	Pole	Lower palm	Upper palm	Tall woody	Short woody	Herbaceous	GRASS-LAND
SUFFRUTESCENT SPECIES											
Acanthaceae	*Justicia secunda* Vahl	–	–	+	+	+	+	–	–	+	+
Campanulaceae	*Centropogon cornutus* (L.) Druce	–	–	–	–	–	–	–	+	+	–
Ochnaceae	*Sauvagesia erecta* L.	–	–	–	–	–	–	–	–	+	+
Oxalidaceae	*Oxalis frutescens* Ruiz & Pavon	–	–	–	–	–	(+)	–	+	+	+
LARGE HERBS											
Bromeliaceae	*Aechmea fendleri* André	+	+	+	+	+	+	–	–	–	–
	Vriesea splendens (Brongn.) Lemée	–	–	+	+	+	+	–	–	–	–
Commelinaceae	?*Commelinopsis persicariifolia* (DC.) Pichon	–	–	?	?	–	–	–	–	–	–
Cyperaceae	*Scleria arundinacea* Kunth	–	–	+	+	+	+	–	–	–	–
	Scleria bracteata Cav.	–	+	+	+	+	+	+	+	+	–
Gramineae	*Andropogon bicornis* L.	–	–	–	–	–	–	–	+	+	+

	Ichnanthus nemoralis (Schrader) Hitchc.	–	–	+	+	+	(+)	–	–	–	–
	Lasiacis anomala Hitchc.	–	–	+	+	+	+	+	–	–	–
	Lasiacis ligulata Hitchc. & Chase	–	–	+	+	+	+	+	–	–	–
	Olyra cordifolia H.B.K.	–	+	+	+	+	–	–	–	–	–
Marantaceae	Maranta arundinacea L.	–	–	+	+	+	–	–	–	–	–
Musaceae	Heliconia caribaea Lam.	–	–	+	+	+	–	+	–	–	–
	Heliconia psittacorum L.f.	–	–	+	+	–	–	–	–	–	–
Piperaceae	Peperomia glabella (Sw.) A. Dietr.	+	+	+	+	+	–	–	–	–	–
Urticaceae	Pilea involucrata (Sims) Urban	–	+	–	–	+	–	–	–	–	–
SMALL HERBS											
Cyperaceae	Eleocharis geniculata (L.) Roemer & Schultes	–	–	–	–	–	–	–	–	+	+
	Fimbristylis complanata (Retz.) Link	–	–	–	–	–	–	–	–	–	+
	Rhynchospora barbata (Vahl) Kunth	–	–	–	–	–	–	–	–	–	+
	Rhynchospora candida (Nees) Boeckeler	–	–	–	–	–	–	–	–	–	+
	Rhynchospora gracilis Vahl	?	?	?	?	?	?	?	?	?	?
	Rhynchospora nervosa (Vahl) Boeckeler	+	+	+	+	+	+	+	–	–	–
	Rhynchospora rugosa (Vahl) Gale	–	–	–	–	–	–	–	–	–	+

TABLE 1 (*continued*).

		TRANSITION FOREST		CLOUD FOREST				WET THICKET			
		with *Clusia rosea*	without *Clusia rosea*	Tall	Pole	Lower palm	Upper palm	Tall woody	Short woody	Herbaceous	GRASS-LAND
	Scleria lithosperma (L.) Sw.	?	?	+	+	+	+	?	?	?	?
	Sp. indet. 1	-	-	-	-	-	-	-	-	-	+
	Sp. indet. 2	-	-	-	-	-	-	-	-	-	+
	Sp. indet. 3	-	-	-	-	-	+	-	-	-	-
Gentianaceae	*Coutoubea spicata* Aublet	-	-	-	-	-	-	-	-	-	+
	Voyrea aphylla Pers.	-	-	+	+	+	+	-	-	-	-
Gramineae	*Andropogon leucostachys* Kunth	-	-	-	-	-	-	-	-	+	+
	Fimbristylis autumnalis (L.) Roemer & Schultes	?	?	?	?	?	?	?	?	?	?
	Ichnanthus pallens (Sw.) Munro	-	(+)	+	+	+	+	(+)	-	-	-
	Pharus latifolius L.	-	-	+	+	-	-	-	-	-	-
Iridaceae	*Trimezia martinicensis* (Jacq.) Herbert	-	-	-	-	-	-	-	-	-	+
Orchidaceae	*Encyclia pygmaea* (Hooker) Dressler	-	-	-	-	-	-	-	-	-	+

	Erythrodes venezuelana Garay & Dunsterv.	-	-	+	+	+	+	-	-	-	-
	Eulophidium maculatum (Lindley) Pfitzer	+	+	+	-	-	-	-	-	-	-
	Spiranthes adnata (Sw.) Bentham	-	-	+	+	+	+	-	-	-	-
CLIMBERS											
Apocynaceae	Mandevilla subsagittata (Ruiz & Pavon) Woodson	-	-	-	+	+	-	-	-	-	-
Asclepiadaceae	Cynanchum parviflorum Sw.	-	-	-	-	-	-	-	+	+	-
	Ditassa oxyphylla Turcz.	-	-	-	-	-	-	-	+	+	-
	Matelea cf. humboldtiana Spellman & Morillo	-	-	+	-	-	-	-	-	-	-
Bignoniaceae	Macfadyena unguis-cati (L.) A. Gentry	+	+	-	-	-	-	-	-	-	-
	Phryganocydia corymbosa (Vent.) Bur. ex Schumann	+	+	-	-	-	-	-	-	-	-
Compositae	Mikania johnstonii Robinson	-	-	-	-	?	?	-	-	-	-
Dioscoreaceae	Dioscorea polygonoides Humb. & Bonpl. ex Willd.	-	-	+	+	+	+	-	-	-	-
Gentianaceae	Drymonia serrulata (Jacq.) Martius	+	+	-	-	-	-	-	-	-	-
Leguminosae	?Bauhinia sp.	+	+	-	-	-	-	-	-	-	-

TABLE 1 (*continued*).

		TRANSITION FOREST		CLOUD FOREST				WET THICKET			
		with *Clusia rosea*	without *Clusia rosea*	Tall	Pole	Lower palm	Upper palm	Tall woody	Short woody	Herbaceous	GRASS-LAND
	Machaerium robiniifolium Vogel	+	+	–	–	–	–	–	–	–	–
Malpighiaceae	*Heteropterys laurifolia* (L.) Juss.	+	+	+	+	+	+	(+)	–	–	–
	Heteropterys macrostachya Juss.	–	–	+	+	(+)	–	–	–	–	–
Passifloraceae	*Passiflora cyanea* Masters	–	–	–	–	–	(+)	+	+	–	–
	Passiflora laurifolia L.	–	–	+	+	+	–	–	–	–	–
Polygalaceae	*Securidaca* cf. *diversifolia* (L.) Blake	+	+	–	–	–	–	–	–	–	–
	Securidaca cf. *volubilis* L.	–	+	–	–	–	(+)	–	–	–	–
Rubiaceae	*Emmeorhiza umbellata* (Sprengel) Schumann	–	–	–	–	+	+	+	–	–	–
Sapindaceae	*Serjania* sp.	+	+	+	+	–	–	–	–	–	–
Smilacaceae	*Smilax* cf. *solanifolia* A. DC.	–	–	+	+	+	+	–	–	–	–
SCANDENT PLANTS											
Compositae	*Mikania trinitaria* DC.	–	–	–	–	+	–	–	–	–	–

	Wedelia caracasana DC.	-	-	-	-	-	(+)	+	+	-	-
	Wedelia fruticosa DC.	-	-	-	-	-	-	-	+	+	-
	Wulffia baccata (L.f.) Kuntze	+	+	+	+	+	+	+	+	-	-
Solanaceae	Solanum lancifolium Jacq.	+	+	+	+	+	+	+	-	-	-
WOODY HEMIEPIPHYTES											
Ericaceae	Vaccinium latifolium Bentham & Hooker f.	-	-	-	-	+	+	+	+	-	-
Marcgraviaceae	Norantea guianensis Aublet	-	+	+	+	-	-	+	+	-	-
Rubiaceae	Hillia parasitica Jacq.	-	-	-	-	-	+	+	+	-	-
EPIPHYTES											
Araceae	Anthurium cf. hookeri Kunth	+	+	+	+	+	+	-	-	-	-
	Philodendron cf. aristeguietae Bunting	-	-	+	-	-	-	-	-	-	-
	Philodendron sp.	+	+	+	+	+	+	+	-	-	-
Bromeliaceae	Glomeropitcairnia erectiflora Mez	-	-	-	-	-	(+)	+	++	+	-
	Guzmania lingulata (L.) Mez	-	-	+	+	+	(+)	-	-	-	-
	Guzmania cf. lychnis L.B. Smith	-	-	-	-	+	-	-	-	-	-
	Guzmania monostachya (L.) Rusby ex Mez	+	+	-	-	-	-	-	-	-	-
	Tillandsia lescaillei Wright	-	-	-	-	-	+	-	-	-	-
	?Tillandsia sp.	-	-	+	-	-	-	-	-	-	-

TABLE 1 (*continued*).

		TRANSITION FOREST		CLOUD FOREST				WET THICKET			
		with Clusia rosea	without Clusia rosea	Tall	Pole	Lower palm	Upper palm	Tall woody	Short woody	Herbaceous	GRASS-LAND
	Vriesea johnstonii Mez	–	–	?	?	?	?	–	–	–	–
	Vriesea simplex (Vell.) Beer	–	–	?	?	?	–	–	–	–	–
Cactaceae	Rhipsalis cf. baccifera (J.S. Miller) Stearn	+	–	–	–	–	–	–	–	–	–
Lentibulariaceae	Utricularia alpina Jacq.	–	–	–	–	+	+	+	–	–	–
Orchidaceae	Campylocentrum micranthum (Lindley) Rolfe	–	–	–	+	–	–	–	–	–	–
	Dichaea graminoides (Sw.) Lindley	–	–	?	?	?	?	–	–	–	–
	Dichaea muricata (Sw.) Lindley	–	–	+	+	+	+	+	–	–	–
	Dichaea picta Reichb. f.	–	–	+	+	+	+	(+)	–	–	–
	Elleanthus arpophyllostachys Reichb.	–	–	+	+	+	+	–	–	–	–
	Epidendrum anceps Jacq.	–	–	–	–	–	–	–	–	?	–
	Epidendrum cochleatum L.	?	?	?	–	–	–	–	–	–	–
	Epidendrum johnstonii Ames	–	–	–	–	–	+	+	–	–	–
	Epidendrum nocturnum Jacq.	–	–	+	+	+	+	+	+	+	+

Epidendrum rigidum Jacq.	–	–	–	–	–	–	–	–	–	?
Epidendrum secundum Jacq.	–	–	–	–	–	–	–	+	+	+
Huntleya lucida (Rolfe) Rolfe	–	–	?	?	–	–	–	–	–	–
Jacquiniella globosa (Jacq.) Schlechter	?	?	?	–	–	–	–	–	–	–
Maxillaria venusta Lindley & Reichb. f.	–	–	–	–	+	+	(+)	–	–	–
Maxillaria virguncula Reichb. f.	–	–	?	?	–	–	–	–	–	–
Platystele johnstonii (Ames) Garay	–	–	–	–	+	+	+	–	–	–
Pleurothallis discoidea Lindley	–	–	+	+	+	+	–	–	–	–
Pleurothallis floribunda (Lindley) Lindley	–	–	?	?	?	?	–	–	–	–
Pleurothallis foliata Griseb.	–	–	?	?	?	?	–	–	–	–
Pleurothallis revoluta (Ruiz & Pavon) Garay	–	–	–	–	–	+	+	–	–	–
Pleurothallis ruscifolia (Jacq.) R. Br.	–	–	+	+	+	+	–	–	–	–
Pleurothallis sclerophylla Lindley	–	–	–	–	–	–	–	–	?	?
Pleurothallis velaticaulis Reichb. f.	–	–	+	+	+	+	–	–	–	–
Pleurothallis sp.	–	–	+	+	+	+	–	–	–	–

Key to symbols: ++ = abundant, + = common, (+) = rare, – = absent, ? = uncertain (refers mainly to authenticated records of species not encountered in the present study).

TABLE 2. **Soil chemistry in the principal vegetation types of Cerro Copey.***

Vegetation type & soil depth (cm)	pH	Carbon (%)	Available P (µg/g)	Total N (mg/g)	Cation exchange capacity	Ca	K	Mg	Na
					(milliequivalents/100g)				
Transition Forest									
0–5	6.85	11.96	4.93	8.47	38.14	22.95	0.026	18.83	1.318
20–30	6.25	2.63	0.73	2.45	13.53	0.97	0.058	16.70	0.912
Cloud Forest									
0–5	4.95 – 5.85	3.17 – 8.79	0.80 – 2.89	2.38 – 4.97	24.67 – 35.71	5.55 – 15.60	0.276 – 0.630	4.53 – 9.10	0.328 – 0.627
15–20	5.45 – 5.65	1.93 – 2.27	0.43 – 2.40	1.40 – 2.45	11.30 – 21.72	1.44 – 3.99	0.090 – 0.142	1.57 – 3.84	0.175 – 0.254
Wet Thicket									
0–5	4.95 – 5.10	4.08 – 20.29	1.10 – 12.20	2.45 – 13.96	21.30 – 44.76	1.63 – 27.00	0.057 – 0.905	1.94 – 15.20	0.157 – 1.529
10–20	5.45 – 5.70	3.35 – 3.62	0.85 – 2.26	2.38 – 3.50	13.53 – 22.6	3.77	0.101 – 0.297	4.40 – 5.53	0.342 – 0.351
Grassland									
0–5	5.60	1.81	2.53	1.33	10.71	1.34	0.065	1.21	0.122
15–20	5.55	1.00	1.50	0.84	12.76	0.69	0.026	0.69	0.081

* Analysis by Centro de Ecología, IVIC, Caracas.

TABLE 3. **Summary of the physiognomic and floristic characteristics of the vegetation types of Cerro Copey.***

Vegetation type	Canopy height (m)	Maximum DBH (cm)	Deciduous trees	Woody lianas	Vascular epiphytes	Bryophytes	Under-story herbs	Palms	Under-story shrubs	Mean leaf area (cm^2)
Transition Forest										
+ Clusia rosea	15 - 30	75	+	++	(+)	-	(+)	-	(+)	29.2
- C. rosea	10 - 15	40	+	++	(+)	-	(+)	(+)	(+)	
Cloud Forest										
Tall	15 - 22	75	(+)	+	+	+	++	+	+	
Pole	13 - 16	35	(+)	+	+	+	+	+	+	23.0
Lower palm	10 - 12	30	(+)	(+)	++	++	+	++	++	
Upper palm	6 - 9	25	(+)	-	++	++	+	++	(+)	
Wet Thicket										
Tall	3 -4	15	-	-	+	+	-	-	-	
Short woody	1 - 2	10	-	-	+	+	-	-	-	12.3
Herbaceous	0.5 - 1	n.a.	-	-	-	(+)	-	-	-	
Grassland	<0.5	n.a.	n.a.	n.a.	n.a.	(+)	n.a.	n.a.	n.a.	n.a.

* Symbols as in Table 1.

FIGURE 4. Transition Forest with *Clusia rosea*.

The irradiance in the understory and on the forest floor is greater than under *Clusia rosea,* and the undergrowth is more dense. Although the lower layers consist mainly of saplings of canopy tree species, there are also a few species of subcanopy trees, notably *Myrciaria* sp. and *Esenbeckia pilocarpoides.* Shrubs are rare. Herbaceous cover is sporadic; clumps of the sedge *Rhynchospora nervosa* occur in shaded gullies, and in places there are dense patches of the spiny bromeliad *Aechmea fendleri.*

Epiphytes, as in the other subtype of Transition Forest, are not abundant. They include the large-leaved *Anthurium hookeri,* a dwarf form of *Aechmea fendleri,* and an additional bromeliad, *Guzmania monostachya,* which is often abundant on exposed knolls close to the lower limit of the Transition Forest. Woody and herbaceous climbers are more frequent than under *C. rosea,* although the species composition is similar.

2. Cloud Forest. Cloud Forest is distinguished from Transition Forest by a far greater abundance of vascular epiphytes, bryophytes, and herbaceous ground cover, by the presence of palms, and by the decreased frequency of deciduous trees. The range of leaf sizes is narrower than in Transition Forest; all the trees have either notophylls or microphylls (Sugden, 1985). Cloud Forest occupies an altitudinal band 250–350 m wide that extends to the summits and ridges on the leeward side of the mountain (Figure 3).

The soils vary considerably in depth. On gentle slopes at lower altitudes (600–700 m), the profile may be up to 200 cm deep, while on steeper slopes near the summit the soil depth is usually no more than 40–50 cm and often as little as 20–30 cm. The litter and fermentation layers are more or less continuous but thin (normally less than 2 cm); deeper accumulations of litter and humus are sometimes found between boulders and among emergent roots. There is no distinct zonation in the mineral horizons, except for a gradual change (in the deeper soils) from a dull humic brown to reddish brown with increasing depth. At higher altitudes the mineral horizons become more clayey, and there is an increased concentration of roots in the upper 5 cm of soil, with fine roots often penetrating the litter layer. In the deeper soils, a discontinuous, hard, nodular layer is often encountered at depths of 70–120 cm. Despite the considerable structural variation in the Cloud Forest soils, there is relatively little variation in their chemistry (see Table 2).

There are four subtypes of Cloud Forest:

a. **Tall cloud forest.** This is undoubtedly the most species-rich of all the evergreen upland vegetation types, with a comparatively high diversity of all lifeforms. Together with pole cloud forest (see below), it occupies the lower part of the altitudinal band of Cloud Forest; its lower limit is contiguous with Transition Forest, and its upper limit rarely exceeds 700 m even on leeward slopes. The height of the canopy ranges from 15 to 22 m, with trees attaining girths of up to 200 cm. Tall cloud forest is best developed in gullies sheltered from the wind.

Most of the tree species and individuals are evergreen, although the deciduous *Croton xanthochloros* and *Tabebuia chrysantha* (particularly the former) are frequent. The most abundant tree species are *Licania membranacea, Guapira*

FIGURE 5. Understory of tall cloud forest, showing abundant *Adiantum tetraphyllum*.

cf. *fragrans, Marlieriopsis eggersii, Myrcia* cf. *coriacea,* and *Maytenus karstenii.* The trees are generally upright, except on the steeper slopes, where they often lean downhill. Larger individuals of *Terminalia amazonia,* also an abundant species, sometimes have small buttresses. The understory is composed mainly of the saplings of canopy trees, especially *Guapira* cf. *fragrans* and *Myrcia* cf. *coriacea.* Subcanopy trees, including *Esenbeckia grandiflora, Guettarda odorata, Myrciaria* sp., and the palms *Euterpe karsteniana* and *Bactris falcata,* are frequent but not abundant. Prominent shrubs include *Psychotria muscosa, Solanum nudum,* and *Cestrum* sp. Large herbs, especially *Heliconia psittacorum, Maranta arundinacea, Aechmea fendleri,* and *Vriesea splendens,* are common; the most abundant one is *Adiantum tetraphyllum* Humb. & Bonpl. ex Willd. (FIGURE 5), the fronds of which arise singly from a creeping underground rhizome. Small herbs, including several grass and orchid species, are frequent (see TABLE 1).

Vascular epiphytes are mostly herbaceous and are confined mainly to the lower boles and branches, where they are abundant. Orchids (*Pleurothallis* spp., *Epidendrum* spp.), bromeliads (*Guzmania lingulata, Vriesea splendens*), aroids (*Anthurium hookeri, Philodendron* spp.), and ferns are well represented. Epiphytic bryophytes, especially the festoon-forming species such as *Taxilejeunea pterogonia* (Lehm. & Lindenb.) Schiffner, *Macromitrium cirrosum* (Hedwig) Bridel, *Orthostichopsis crinita* (Sulliv.) Broth., and *Phyllogonium fulgens* (Hedwig) Brid., and filmy ferns are patchily distributed; some boles have a substantial (up to 80%) covering, while others are more or less naked. Woody hemiepiphytes are present, although uncommon; *Clusia rosea* and *Ficus nymphaeifolia* occasionally occur, as do some of the hemiepiphytes (*Blakea monticola, Clusia* cf. flava, *Hillia parasitica, Norantea guianensis*) common in the Wet Thicket (see below) at higher altitudes. Epiphylls are evident for the first time in this altitudinal sequence of vegetation types. The older, shaded foliage of saplings and understory palms is often thickly encrusted with lichens and hepatics.

Woody climbers are frequent, represented almost exclusively by *Heteropterys laurifolia* and *H. macrostachya,* the latter easily recognized by the silvery, densely tomentose lower leaf surfaces. Both of these species are common in the understory in their preclimbing, straggling-shrub stage; when adult, their stems reach a maximum diameter of 2–3 cm. The scandent sedge *Scleria bracteata,* climbing by means of its minutely barbed leaf surfaces, frequently festoons the more open parts of the understory.

b. **Pole cloud forest.** This subtype extends over a range of altitudes similar to those of the tall cloud forest, differing from the latter in its lower stature (13–16 m), higher density of trees, and lower maximum bole girth (rarely more than ca. 100 cm) (see FIGURE 6). The term "pole" reflects the absence of trees of large girth. Pole cloud forest generally occurs on gentle slopes exposed to the prevailing winds, and its trees are mostly upright, with dense crowns. The crowns are often separated from their neighbors by clear spaces caused by mutual abrasion in the wind (FIGURE 7). The tree flora is very similar in composition to that of the tall cloud forest, although relative abundances are

FIGURE 6. Interior of pole cloud forest.

somewhat different (Sugden, in preparation); in particular, *Licania membranacea* is less common, and *Guapira* cf. *fragrans* and *Myrcia* cf. *coriacea* more common.

The woody understory is very similar to that of the tall cloud forest, with saplings of *Guapira* cf. *fragrans* and *Myrcia* cf. *coriacea* especially abundant. Shrubs and large herbs have a lower diversity, with the former represented

FIGURE 7. Canopy of pole cloud forest from below, showing mutual abrasion of neighboring crowns.

almost exclusively by *Psychotria muscosa,* and the latter by *Maranta arundinacea, Vriesea splendens,* and *Adiantum tetraphyllum.* There are also fewer species of small herbs.

The epiphytic flora is less luxuriant than that of the tall cloud forest, although there are no marked floristic differences. Again, the majority of the epiphytes are found in the shaded understory layers. Festooning bryophytes are less common, and these and the filmy ferns frequently dry out in spite of regular cloud cover.

Heteropterys laurifolia and *H. macrostachya* are again the most abundant woody climbers, and as in the tall cloud forest the juvenile individuals of both species are important components of the lower understory. Mature individuals with their crowns in the forest canopy rarely have stem diameters exceeding ca. 2 cm.

c. **Lower palm forest.** As its name implies, palm forest can be distinguished from the two previous Cloud Forest subtypes by a greater abundance of the palm *Euterpe karsteniana.* The height of the forest is reduced to 10–12 m, and *E. karsteniana* becomes an important component of the canopy, rather than a subcanopy tree. The individuals of this species usually have a single bole arising from a small (to ca. 30 cm tall) pyramid of stilt roots, among which there are frequently a number of juvenile shoots.

Lower palm forest occurs in a narrow (ca. 700–750 m) band on the windward slopes of Cerro Copey and in a somewhat wider one (ca. 750–850 m) on leeward slopes. Trees in this forest are smaller in both height and girth than in the

previous Cloud Forest subtypes; boles are generally vertical, but a few lean by up to 20°.

Floristic differences between lower palm forest and the taller Cloud Forest subtypes are few. In the former, *Croton xanthochloros* and *Bactris falcata* are absent or nearly so. *Guapira* cf. *fragrans, Myrcia* cf. *coriacea, Maytenus karstenii,* and *Ilex guianensis* continue to be important components of the canopy.

The understory is generally denser than in the taller Cloud Forests, chiefly due to the abundance of *Psychotria muscosa*; saplings of canopy trees are common but less abundant. The subcanopy tree *Esenbeckia grandiflora* is commoner here than on any other part of the mountains.

Large and small herbs are less well represented, in both diversity and abundance. *Aechmea fendleri* and *Maranta arundinacea,* in particular, are uncommon, although *Adiantum tetraphyllum* occurs frequently. The understory and substrate are permanently damp, and the exposed boulders, roots, and fallen boles have a covering of mat- and cushion-forming bryophytes, especially *Leucobryum giganteum* C. Mueller and *L. antillarum* Schimper ex Besch.

The vascular epiphytic flora is similar in diversity and abundance to that of the tall cloud forest, except that the woody hemiepiphytes are more frequent. Epiphytic bryophytes, as on the substrate, are better developed than in the previous subtypes. Woody climbers, by contrast, are rare.

d. **Upper palm forest.** The last of the Cloud Forest subtypes, which extends to the summit of Cerro Copey on the leeward side, is distinct from lower palm forest in its lesser stature (6–9 m) and in the inclination of the trees (see FIGURE 8). Most boles are strongly (20–90°) inclined downhill, and they are frequently twisted and gnarled, branching at all levels in the forest profile. As a result of this habit and the generally boulder-strewn terrain, progress through upper palm forest is far more difficult than through the other forest types. Nevertheless, the principal components of the canopy are very similar to those of the lower palm forest, the only notable absentees being *Licania membranacea* and *Esenbeckia grandiflora.* Individuals of *Euterpe karsteniana* have more massive (up to 1 m tall and 70 cm across at the base) stilt-root systems and often have up to six shoots of canopy height as well as numerous juvenile shoots among the roots.

The understory is quite different from that of the lower palm forest. Shrubs are almost absent, and the density of young saplings is low. *Adiantum tetraphyllum* is present, although at a relatively low density, while *Aechmea fendleri* occurs more frequently than on any other part of the mountain, forming extensive spiny groves that contribute to the general impenetrability of the forest. Abundant scandent shoots of *Scleria bracteata,* with minutely serrated leaves and sheaths, supply an additional irritant and impediment to progress through the forest. Small herbs are few, represented chiefly by *Ichnanthus* sp., *Spiranthes adnata,* and *Elaphoglossum* sp. The boulders, lower boles, and exposed roots are covered with thick cushions of *Leucobryum giganteum* and *L. antillarum*; as in the lower palm forest, the understory is perpetually damp except in places where the canopy is thin and broken.

The epiphytic flora is notable for a much greater abundance of woody hemi-

FIGURE 8. Interior of upper palm forest, showing abundant bryophytes and leaning trees.

epiphytes (e.g., *Hillia parasitica, Clusia* cf. *flava*), which often form thick, tangled masses in the upper canopy. The flora of herbaceous epiphytes is similar in composition to that at lower altitudes, except for an increased frequency of the large bromeliad *Glomeropitcairnia erectiflora*. Woody climbers are entirely absent.

3. WET THICKET. Wet, windswept thickets less than 4 m tall dominate the windward slopes of Cerro Copey from ca. 800 m to the summit. They are distinguished from upper palm forest by their lesser stature, the absence of palms, and the reduced diversity and density of herbaceous epiphytes and bryophytes. The woody canopy plants are mostly microphyllous, and their leaves are significantly thicker than those of their counterparts in the Cloud Forest (Sugden, 1985).

The soils of the thickets are quite shallow—usually less than 40 cm deep. The litter layer is discontinuous, and the fermentation layer is barely discernible except where pockets of humus accumulate between boulders and large superficial or raised roots. Normally the top 15–20 cm is a coherent, wet, pale red-brown silty clay containing fragments of rotting leaves. The remainder of the profile, which gradually gives way to rock fragments and finally to bedrock at 30–40 cm depth, is more silty, more readily fragmented, and pale brown. Roots are sparse throughout, in contrast to their distribution in the forest soils, and wormcasts provide evidence of considerable animal activity. Although slightly more acidic (pH 4.95–5.70) than the Cloud Forest soils, the Wet Thicket soils display no chemical properties markedly different from those of the other upland soils (see TABLE 2).

There are three subtypes of Wet Thicket:

a. **Tall thicket.** This vegetation, which has a lower limit contiguous with upper palm forest on the windward slopes, is characterized by a canopy 3–4 m tall, an absence of boles more than ca. 10 cm in diameter, and an abundance of *Clusia* cf. *flava* (see FIGURE 9). Most of the woody species of the Cloud Forest are present in stunted form, but *C.* cf. *flava* is clearly the dominant species, forming extensive pure stands. *Blakea monticola* is also very common. Tall thicket has no discernible understory but is almost impenetrable due to the tendency of *C.* cf. *flava* to retain its dense branches at all levels. A hemiepiphyte, this species often has no discernible bole, and individuals are frequently much broader than tall. There are a small number of saplings, no shrubs, and few herbaceous species apart from *Scleria bracteata*. Herbaceous vascular epiphytes occur infrequently compared to the levels observed in the Cloud Forest; one of the common species in the tall thicket is the endemic orchid *Epidendrum johnstonii*. Bryophytes are much less abundant than in the palm forests, in spite of the permanent wetness of the boles and lower branches; generally, there is only a thin covering of creeping mosses and slimy algae.

Tall thicket occurs on all the slightly less exposed parts of the upper windward slopes of Cerro Copey and is also present in a narrow band a few meters wide along the ridges dividing the windward slopes from the leeward, where it forms the ecotone between the short thickets (see below) and the upper palm forest.

b. **Short woody thicket.** This vegetation differs from tall thicket in its lesser stature (1–2 m), its more even abundance of woody species, and its greater profusion of large herbs. *Clusia* cf. *flava* is still very common, but markedly stunted forms of Cloud Forest canopy tree species are much more frequent than in the tall thicket (see FIGURE 10). The large tank bromeliad *Glomeropitcairnia erectiflora* is a very prominent feature of this vegetation, usually

FIGURE 9. Canopy of tall thicket, showing *Clusia* cf. *flava* (Cf) and *Blakea monticola* (Bm).

FIGURE 10. Canopy of short woody thicket, showing abundant *Clusia* cf. *flava,* and flowering individuals of *Glomeropitcairnia erectiflora* (horizon).

growing epiphytically with its yellowish foliage fully exposed in the canopy. The trunkless tree fern *Cnemidaria grandifolia* (Willd.) Proctor is common here. *Scleria bracteata,* with very reduced internodes, is abundant. As in the tall thicket, most of the smaller forest herbs and epiphytes are absent. Interestingly, a high proportion of all species in the short woody thicket appear to germinate epiphytically, especially in the accumulations of organic matter in the axils of the dead basal leaves of individuals of *Glomeropitcairnia erectiflora.*

Short woody thicket dominates the most-exposed slopes near the principal

FIGURE 11. Grassland at 900 m on Cerro Copey.

ridges and summits of Cerro Copey. Progress through this vegetation is exceptionally difficult. The ground is invisible, there is nothing substantial to grasp hold of, the leaves and stems of *Scleria bracteata* lacerate the skin, and large bromeliads empty tankfuls of water into one's boots. In addition, a gale blows almost perpetually.

c. **Herbaceous thicket.** The last of the three Wet Thicket subtypes consists mainly of herbs 0.5–1 m tall. Floristically, it is not dissimilar to the herbaceous component of the short woody thicket. *Glomeropitcairnia erectiflora* is again abundant, and *Scleria bracteata* often occurs in extensive pure stands. The ferns *Dicranopteris flexuosa* (Schrader) Underw. and *Pteridium aquilinum* L. are frequent. Orchids, particularly *Epidendrum nocturnum* and *E. secundum,* occur as isolated individuals or in small clumps. Woody species are present but not abundant and do not constitute the main structural component of the vegetation. They include scandent or loosely branched shrubs such as *Wedelia caracasana, Centropogon cornutus,* and *Clidemia hirta*; suffrutescent species such as *Oxalis frutescens* and *Sauvagesia erecta*; and occasional individuals of stunted trees, especially *Rapanea guianensis, Myrcia* cf. *coriacea,* and *Roupala montana.*

Herbaceous thicket occupies sites similar in aspect, topography, and altitude to those inhabited by short woody thicket.

4. GRASSLAND. Grassland (FIGURE 11) is by far the most restricted vegetation type of all those described here, occurring in a few patches of several hundred square meters close to the summit of Cerro Copey in moderately sheltered sites. It warrants consideration as a separate vegetation type due to the absence of the large, coarse herbs that dominate the herbaceous thicket, and to the presence of smaller herbaceous species that are rare or absent in other vegetation types. The most abundant species, which was never observed to flower and hence remains undetermined, appears to be a species of *Trachypogon.* Clumps of *Andropogon bicornis* and *A. leucostachys,* and of several small sedges, are frequent. *Scleria bracteata* is absent. There is no evidence to suggest that the Grassland represents sites of earlier disturbances.

Grassland soils are typically drier than any of the Wet Thicket ones, and the mineral horizons are distinctly silty. The litter and fermentation layers are very thin, and the carbon content at the top of the profile is low compared to that of the other soils (see TABLE 2). Small stones are distributed throughout the profile, and the overall depth rarely exceeds 50–60 cm.

Ecotones and Variations

The boundaries between the various vegetation types and subtypes range from abrupt to gradual, and it is always possible to find intermediate types. Abrupt ecotones are generally found between the two subtypes of Transition Forest, between Cloud Forest and Wet Thicket, and between Wet Thicket and Grassland. The ecotones within the Cloud Forest and the Wet Thicket are characteristically more gradual, except where they accompany sharp changes in topography (e.g., on the main ridge of Cerro Copey—see FIGURE 12). Zo-

FIGURE 12. Main ridge of Cerro Copey, looking southeast, showing contrast between windblown vegetation (right) and sheltered vegetation (left).

nation of the vegetational subtypes tends to be more marked on the windward slopes; on leeward slopes, there is more intergradation, the canopy is less dense, and epiphytes are usually less abundant.

There are patches of vegetation that do not correspond well to the scheme outlined above, but these are limited in extent. For example, areas more or less devoid of palms can be found within the lower and upper palm forests, while other floristic and physiognomic criteria remain unchanged. On exposed knolls in the pole cloud forest, canopy height is sometimes reduced to as little as 10 m, but this reduction is not associated with features of the stunted vegetation at higher altitudes. Patches of upper palm forest with an open and broken canopy—and a correspondingly well-lit understory with abundant *Scleria bracteata* and relatively few epiphytes—occur on the leeward sides of some of the principal ridges.

Gaps in the canopy caused by falling trees are a common feature of the taller Cloud Forest subtypes. Gaps are smaller and less frequent in the palm forests and are (obviously) absent from the Wet Thicket. An interesting characteristic of many of the gaps is that the uprooted tree does not die but produces epitrophic shoots from the fallen bole, some or all of which may eventually reach the canopy and also become rooted independently.

Human activity in the evergreen vegetation of Cerro Copey appears to have been limited. Of all the vegetation types described here, only Transition Forest may have been subject to significant disturbance in the past, partly due to selective felling for construction materials and partly due to goats, which have been far more numerous on the island than they are at present. Cerro Copey is now a National Park, and cutting of the vegetation above 100 m is prohibited. Nevertheless, the construction of the summit road in the early 1970's, and the attendant disturbances, has led to the invasion of a considerable number of weedy species, mostly from the lower slopes. These species, listed in the APPENDIX, are presently confined largely to roadsides and the landslides provoked during construction.

Vegetation of Matasiete, Guayamurí, and Tragaplata

On Cerros Matasiete and Tragaplata, which are similar to each other in size, there is a compression and mixing of the vegetation types seen on Cerro Copey. The limit of Transition Forest on these mountains is lower. *Clusia rosea* Transition Forest is especially well developed, and aerial photographs clearly show that it occupies at least 50 percent of the total area above 350 m on both mountains. At the upper limit of the Transition Forest on the leeward slopes (550–600 m), there is a much more marked and sudden increase in wetness than on Cerro Copey, and vascular epiphytes and festooning bryophytes become abundant quite suddenly. This narrow band of Cloud Forest between the Transition Forest and the highest ridges has the physiognomy of lower palm forest, but with a low frequency of palms. On the windward sides of the ridges and summits, there is a wide band of tall woody thicket with abundant *Clusia* cf. *flava,* and on Cerro Tragaplata there is also a small area of short woody thicket close to the summit. Neither peak supports any Grassland.

Cerro Guayamurí supports near its summit a curious mixture of Transition Forest, Cloud Forest, and Wet Thicket, with a physiognomy that can only be described as patchy and apparently disorganized. The area of the upper slopes is so small (less than 20 ha) and the topography so rugged that there is no clear zonation. The summit, although less than 500 m high, is very moist, and epiphytes including festooning bryophytes are abundant. In the apparent absence of *Clusia* cf. *flava,* the Wet Thicket on the windward slopes is a tangled mass of wind-pruned trees, especially *Guapira* cf. *fragrans, Clusia rosea,* and *Calliandra panlosia.*

The upper slopes of these three mountains are not sufficiently well explored for accurate floristic comparisons to be made with Cerro Copey. It is clear, nevertheless, that the overall species richness (especially on Cerro Guayamurí) is less than that on Cerro Copey. In general, species that are common on Cerro Copey (except for the Wet Thicket species) are also present on Matasiete and Tragaplata, although not necessarily on Guayamurí; notable absentees from the latter include palms and many of the epiphytic species. No species has been encountered on any of the smaller mountains that is not known from Cerro Copey.

Upland Vegetation of Macanao

The western mountains of Margarita, on the peninsula of Macanao, support a series of vegetation types that are interestingly different from those of Cerro Copey and its smaller satellites. Although the principal peaks of Macanao—Soledad and Los Cedros—are as high as Matasiete and Tragaplata, and although there is a trend toward increasingly evergreen vegetation with higher altitude, there is no vegetation that approaches that of the eastern mountains in terms of wetness or abundance of epiphytes.

The highest parts of the Macanao mountains are best ascended from the village of San Francisco, which is situated at the mouth of a steep valley on the northern side of the range. To within 100 m of the principal summit (Los Cedros), the steep slopes are clothed in deciduous woodland of varying height

and density. *Bursera simaruba* (L.) Sarg. and *Ceiba pentandra* are common trees, reaching heights of up to 15 m. In previous times *Cedrela* sp. was abundant, but it has been mostly removed over the past century for timber. In the gullies and on some of the more sheltered slopes, there are more evergreen trees, especially species of Capparidaceae. Limited areas have been cleared for the cultivation of mango and manioc, but neither crop is very successful due to the very sporadic rains. Columnar cacti are a prominent feature of all the slopes, particularly in the deciduous woodland; old, much-branched individuals of *Ritterocereus* sp. attain heights of up to 12 m. At higher altitudes, a scandent *Hylocereus* sp. occurs frequently, while at lower levels *Opuntia* spp. and a species of *Melocactus* are common in the ground layer. Epiphytes are infrequent on the dry slopes and are mainly represented by small xeromorphic *Tillandsia* spp.

As one approaches the summit of Los Cedros from the leeward side, there is an abrupt floristic change at ca. 550 m. The deciduous species of the lower slopes are replaced by small, mainly evergreen ones approximately 6–10 m tall, including *Clusia* cf. *minor* L., *Erythroxylum undulatum* Plowman, and *Psidium* sp. Some deciduous species, particularly *Coccoloba* sp., are also present and are confined to this upper zone. Large columnar cacti persist. There is a sudden increase in the frequency of epiphytes; xeromorphic species such as *Rhipsalis* sp., *Campylocentrum micranthum, Anthurium scandens* (Aublet) Engler, and *Tillandsia bulbosa* Hooker are common, and many branches are festooned with bearded lichens.

The vegetation of the summit is sparse and patchy, with stunted wind-pruned trees standing individually or in small groups on an otherwise bare expanse of loose stones and compacted gravel (possibly the result of human intervention). Most of the trees, usually no more than 5 m tall, support a dense epiphytic flora consisting of a mixture of mesomorphic and xeromorphic forms. *Guzmania monostachya,* a small tank species, is abundant on the boles and lower branches; the larger tank species *Vriesea platynema* Gaudich., with water-filled leaf axils, forms substantial colonies on the middle branches, while xeromorphic bromeliads (*Vriesea heterandra* (André) L. B. Smith, *Tillandsia bulbosa,* and *T. kegeliana* Mez) occupy the outermost twigs. In addition, there are several small leathery-leaved orchids and climbing epiphytic ferns.

On the windward side of the summit of Los Cedros, which like all other parts of the mountain is very steep (> 30°), there is a patch of evergreen forest extending some 70–80 m down the slope. In floristic terms this can best be described as an impoverished mix of Transition Forest and Cloud Forest. The commoner trees include *Guapira* cf. *fragrans, Cupania americana, Coccoloba* sp., and *Clusia minor.* There are no palms, and *Clusia rosea* is absent. The epiphytic flora is similar to that of the summit, with such notable additions as *Vriesea splendens, Guzmania lingulata, Anthurium hookeri,* and several large ferns that are present in the shaded understory. As on the lower slopes, there is only a sparse ground cover, and the soil surface is often fully exposed. The litter is dry and discontinuous, and there is a barely discernible fermentation layer covering the mineral soil; the latter has a loose, silty consistency and is pale gray-brown. Small stones, boulders, and outcrops of bedrock are frequent.

This patch of evergreen vegetation, no more than two or three hectares in extent, is being rapidly degraded by local commercial plant collectors.

DISCUSSION

In the Neotropics, montane vegetation that is largely dependent on cloud interception and strongly influenced by wind is a relatively unusual phenomenon. It occurs on two other small mountains on the Caribbean coast of South America, which have been considered in previous articles (Sugden, 1982a, 1982b, 1983); these are Cerro Santa Ana (830 m), on the peninsula of Paraguaná, Venezuela, and the Serranía de Macuira (865 m), on the peninsula of Guajira, Colombia. Of the three, the Margarita mountains have the richest vascular flora and exhibit the most marked physiognomic zonation and variety; nevertheless, the range of physiognomic types in the three localities is essentially similar, with relatively tall forest on sheltered slopes contrasting with low, windswept thickets on the more exposed upper slopes.

Varying levels of exposure to strong, cloud-bearing winds have been shown to have important effects, even if rainfall is high, on the distribution of montane vegetation types elsewhere in the Caribbean region. A good example is the Cordillera de Tilarán, Costa Rica (Lawton & Dryer, 1980), where the cloud flux on the windward slopes results in a richer and denser epiphytic flora than is found on the leeward slopes, even though the annual rainfall is higher (> 2000 mm) and the dry season much shorter (four months) than on Margarita. Wind reduces the canopy height of these forests to 2–8 m near the main ridge of the Cordillera (1850 m), while in sheltered gullies on the leeward side it may attain 30–40 m (Lawton & Dryer, 1980). Persistent wind also affects forest stature on smaller (i.e., ca. 1000 m alt. or less) wet mountains in the region, especially in Panama (Myers, 1969), the Lesser Antilles (Beard, 1944, 1955), and Puerto Rico (Howard, 1968; Baynton, 1969).

In a previous article (Sugden, 1982a) I discussed the question of the classification of the montane vegetation of the Serranía de Macuira. Most of the arguments also apply to the Margarita vegetation and need only be summarized here. The classification scheme of Holdridge (1967) was found to be unsatisfactory for the wetter vegetation types since it does not take into account the effects of cloud interception, seasonality, or persistent high wind. The Cloud Forest on Margarita conforms well to the category of Upper Montane rain forest *sensu* Grubb and Tanner (1976) and can be subdivided according to the scheme of Beard (1955) into "Montane Rain Forest" (pole and tall cloud forest), "Montane Thicket" (lower palm forest), and "Elfin Woodland" (upper palm forest). The palm forests described here are not to be confused with the "Palm Brake" of Beard (1944), which is a formation with a very broken and uneven canopy consisting mainly of palms 15–18 m high and having few, rather scattered, dicot trees of very variable size. Beard (1955) subsequently removed this formation from his classification scheme on the grounds that it is a successional stage following severe disturbance, rather than a relatively stable "climax" formation.

The Wet Thicket of Margarita is best regarded as a specialized, wind-pruned

facies of Upper Montane forest or Elfin Woodland. Neither the Wet Thicket nor the Grassland should be regarded as páramo or "subpáramo" (as they are frequently described on herbarium labels), which are very different formations determined by low temperatures at high altitudes rather than by wind.

The Transition Forest is clearly too dry to conform to the categories of Upper or Lower Montane rain forest. However, it is not dissimilar to the Tropical Dry Forest of Holdridge (1967), a vegetation type that is normally characterized by a mixture of evergreen and deciduous trees with a canopy 15–25 m high, and occurs in lowland areas with mean annual rainfall of 1000–2000 mm. There are also some parallels with the Semi-Evergreen Seasonal forest of Beard (1944), which has a canopy 20–26 m high, a mixture of evergreen and deciduous trees (mostly unbuttressed), and a relative scarcity of epiphytes.

The possible factors that determine the physiognomy of the various montane vegetation types can be summarized as follows. Cloud cover and flux determine the level of the ecotone between the dry vegetation types and the Transition Forest, and increasing cloud flux at higher altitudes sustains a richer and denser epiphytic flora. High winds cause the extreme reduction in stature observed in the Wet Thicket. A combination of wind and a thin, unstable substrate may lead to the reduced stature of upper palm forest on exposed slopes. On leeward slopes a reduction in soil depth at higher altitudes may limit the growth of the trees. In some instances individual species may have a significant effect on the physiognomy of an entire vegetation type, for instance *Clusia rosea* in Transition Forest. All of these possibilities merit further investigation.

Some of the observed trends, including the virtual absence of understory shrubs from the upper palm forest, and the steady decrease with altitude in the density and diversity of woody lianas, have no ready explanations. The latter trend is commonly observed on larger, wet, tropical mountains (cf. Grubb & Tanner, 1976), but it is surprising to find the same phenomenon over such a narrow range of elevations as on Margarita. Since there are relatively few species of either shrubs or lianas in the Margarita forests, the observed trends may reflect the habitat requirements of individual species rather than those of the life-form as a whole.

The relationship between soils and vegetation on the Margarita mountains would repay further investigation. Soils derived from ultramafic rock are often very infertile and inimical to plant growth (Proctor & Woodell, 1975). However, the limited results presented here (TABLE 2) suggest that the montane soils are not particularly infertile, and there is little to indicate that differences in soil chemistry are responsible for the physiognomic variety of the vegetation. All the soils have a pH favorable to plant growth and, with the possible exception of the Grassland soils, have no obvious mineral deficiencies. A high ratio of magnesium to calcium, normally typical of ultramafic soils (Proctor & Woodell, 1975), is found only in the Transition Forest soil.

The montane forests of Margarita clearly provide an interesting opportunity for investigating the factors limiting the distribution of vegetation types on wet tropical mountains. Their existence indicates that the peculiar features of montane forest physiognomy can be achieved at relatively high temperatures, on apparently fertile soil, and in the absence of the constraints imposed by regular

daytime cloud cover. Given these conditions, and the evident versatility of many of the tree species with regard to habitat, the Margarita forests represent a useful, and in a sense experimental, site for further studies. The present account of the vegetation was in part stimulated by Johnston's (1909, p. 281) earlier observation that "there is an interesting field for study in the distribution of the individual species of plants whether in groups or singly, whether in one place or scattered in many, and whether on one slope and not another." The mountains of Margarita are easily accessible, especially since there is now a road to the summit of Cerro Copey, and the natural vegetation is protected from destruction by Venezuelan law. It would be a pity if another 75 years were to elapse before further effort is made to explore the questions raised herein.

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APPENDIX. **Invasive species of roadsides and landslides.**

TREES AND SHRUBS

Boraginaceae	*Cordia curassavica* (Jacq.) Roemer & Schultes
Euphorbiaceae	*Croton populifolius* Miller

Leguminosae	*Mimosa arenosa* Poiret
Moraceae	*Cecropia peltata* L.
Solanaceae	*Solanum asperum* Vahl
	Solanum sp.
Sterculiaceae	*Melochia tomentosa* L.
Ulmaceae	*Trema micrantha* Blume
Verbenaceae	*Lantana camara* L.
	Lantana canescens H.B.K.

CLIMBERS AND SCRAMBLERS

Apocynaceae	Sp. indet.
Compositae	*Calea solidaginea* H.B.K.
	Vernonia moritziana Schultz Bip.
	Vernonia scorpioides (Lam.) Pers.
Convolvulaceae	*Evolvulus sericeus* Sw.
	Jacquemontia nodiflora (Desr.) G. Don
	Jacquemontia pentantha (Jacq.) G. Don
Euphorbiaceae	*Phyllanthus niruri* L.
Leguminosae	*Canavalia oxyphylla* Standley & Williams
	Chaetocalyx scandens (L.) Urban

HERBS AND SUFFRUTESCENT PLANTS

Amaranthaceae	*Achyranthes indica* (L.) Miller
Boraginaceae	*Heliotropium angiospermum* Murray
Campanulaceae	*Isotoma longiflora* (L.) Presl
Compositae	*Bidens pilosa* L.
	Conocliniopsis prasiifolia (DC.) R. M. King & H. Robinson
	Emilia javanica Fosberg
	Eupatorium ballotaefolium H.B.K.
	Pluchea odorata (L.) Cass.
	Psila trinervis (Lam.) Cabrera
	Sonchus asper (L.) Miller
	Sonchus oleraceus L.
Cyperaceae	*Scleria hirtella* Sw.
Euphorbiaceae	*Chamaesyce dioica* (H.B.K.) Millsp.
Gramineae	*Ichnanthus acuminatus* Sw.
	Panicum latifolium L.
	Paspalum conjugatum P. Bergius
	Paspalum fimbriatum H.B.K.
	Paspalum millegrana Schrader
	Paspalum saccharoides Nees
	Polypogon cf. *semiverticillatus* (Forsskål) Hylander
Leguminosae	*Desmodium axillare* (Sw.) DC.
Lythraceae	*Cuphea denticulata* H.B.K.
Orchidaceae	*Habenaria monorrhiza* (Sw.) Reichb. f.
Rubiaceae	*Borreria laevis* (Lam.) Griseb.
	Diodia apiculata (Willd. ex Roemer & Schultes) Schumann
	Diodia teres Walter
	Spermacoce verticillata L.
Verbenaceae	*Stachytarpheta jamaicensis* (L.) Vahl

Note added in proof. A new flora of Margarita Island has recently been published: Hoyos, J. Flora de la Isla Margarita, Venezuela. 927 pp. Monografía no. 34, Sociedad y Fundación La Salle de Ciencias Naturales, Caracas.

NOMENCLATURAL NOTES ON MICONIA (MELASTOMATACEAE)

R. A. HOWARD AND E. A. KELLOGG[1]

The genus *Miconia* Ruiz & Pavon is a conspicuous but nomenclaturally confused element of the Caribbean flora. The early collectors in the region returned with their specimens to different countries, so that any given species was often named several times independently. Most of these early epithets were in the genus *Melastoma* L. For the Caribbean region the most important of the early monographs were those of Desrousseaux (9 Feb. 1797), Richard (1792), Swartz (1788 and 1800), Bonpland (1806–1823), and Vahl (March 1797, and 1807). Vahl's work, in particular, created many nomenclatural problems, since many of his species are renamings of already-published ones. Although the genus *Miconia* was published in 1794, it remained for De Candolle (1828) to make many of the necessary transfers from *Melastoma. Miconia* was subsequently monographed by Triana (1871) and later by Cogniaux (1887–1888, 1891). Cogniaux was somewhat idiosyncratic in his choice of names; his rules of synonymy seem to bear little resemblance to the current *International Code of Botanical Nomenclature.*

This paper accounts for names applied to species and varieties of *Miconia* or *Melastoma* in the Lesser Antilles. We have adopted the modern practice of Gleason, Cogniaux, and Wurdack and consider the genus *Cremanium* D. Don as a section of *Miconia.* Since most species were originally described under the generic name *Melastoma,* all *Melastoma-Miconia* specific epithets are treated in one alphabetic sequence.

A number of species of *Miconia* reported for the Caribbean islands were in fact cultivated in botanical gardens, several of which were established very early in the history of the region. In general, collections attributed to Anderson or Caley can be assumed to have been cultivated at the St. Vincent Botanical Garden, of which both men were sometime directors. Some of Anderson's collecting was done in northern South America. Guilding was historian of the garden and sent his collections to Hooker; his collections contained native as well as cultivated species. Another major botanical garden was in Havana, directed by De La Ossa. Many of his specimens, listed as being from Havana, are actually plants from St. Vincent sent by Anderson and cultivated in Cuba.

In spite of the great profusion of names in the genus, we have found two unnamed taxa, which we name and describe here. We also include keys to the species of *Miconia* native to the Lesser Antilles.

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KEY TO THE LESSER ANTILLEAN TAXA OF MICONIA, WITH VEGETATIVE CHARACTERS EMPHASIZED

1. Leaves with base strongly decurrent along petiole; 5-nerved, outer pair of lateral nerves suprabasal, inner pair joining midrib 5–10 mm above outer. . . *M. prasina.*
1. Leaves with base cuneate, rounded, or cordate, but not decurrent; if 5-nerved then lateral nerves basal, or inner pair inserted < 5 mm above outer.
2. Leaf base cordate with auriculate lobes, almost concealing petiole, leaf thus appearing nearly sessile; petiole < 7 mm long.
3. Largest leaves 7–13 cm long, 3- or 5-nerved.
4. Leaves 3-nerved; margin plane; Dominica. . . . . *M. ernstii.*
4. Leaves 5-nerved; margin strongly inrolled; Martinique. . . . . *M. martinicensis.*
3. Largest leaves 19–40 cm long, 5-nerved. . . . . *M. impetiolaris.*
2. Leaf base cuneate, rounded, or cordate without auriculate lobes; petiole > 7 mm long.
5. Leaves more or less densely tawny-pubescent abaxially.
6. Leaves 5-nerved; inflorescence bracts 6–14 mm long, erect, white, oblong-obovate, enclosing flowers, caducous; petals 6. . . . . *M. mirabilis.*
6. Leaves 3-nerved; inflorescence bracts < 1 mm long, spreading, green to reddish, triangular, persistent; petals 4. . . . . *M. tetrandra.*
5. Mature leaves glabrous or only sparsely pubescent abaxially, the pubescence only visible with lens, not notably tawny.
7. Young stems, leaves, petioles, and inflorescence axes appearing densely furfuraceous to naked eye; inflorescence a narrow thyrse with 2 or 4 branches per node, each branch a pedunculate cyme. . . . . *M. furfuracea.*
7. Young stems, leaves, petioles, and inflorescence axes glabrous or closely appressed-stellate but appearing smooth to naked eye (leaf margins sometimes ciliate, branch nodes sometimes setose); panicles open, spreading, much branched.
8. Leaves with ciliate margins, branches setose at nodes.
9. Leaves with midrib curved abaxially (leaves do not press flat easily), blade with scattered stellate pubescence (denser on abaxial nerves); inflorescence branches secund, often cincinnate; flowers perfect; bracts much shorter than flowers; stigmata flaring. . . . . *M. racemosa.*
9. Leaves with midrib straight, blades glabrous (except for long setae on proximal portion of abaxial veins on some specimens of *M. coriacea*); inflorescence branches not secund; plants dioecious; bracts exceeding flowers; stigmata tacklike.
10. Setae in internodes (density highly variable), as well as more densely at nodes and on petioles; leaf margins strongly reflexed. . . . . *M. coriacea.*
10. Setae restricted to nodes, not in internodes or on petioles; leaf margins plane. . . . . *M. globuliflora* var. *dominicae.*
8. Leaf margins not ciliate and/or branch nodes not setose.
11. Leaves with inner pair of lateral nerves suprabasal; calyx plus hypanthium 1–1.3 mm long.
12. Flowers not secund on inflorescence branches; widespread in Lesser Antilles. . . . . *M. trichotoma.*
12. Flowers secund on inflorescence branches; endemic to St. Lucia. . . . . *M. secunda.*
11. Leaves with inner pair of lateral nerves basal; calyx plus hypanthium > 1.3 mm long, or if less then plant dioecious and leaves cartilaginous-denticulate.

13. Leaves dentate, denticulate, or serrate.
    14. Upper internodes mostly < 2 cm long; plants dioecious; bracts oblanceolate, exceeding flowers; stigmata tacklike.
        15. Branches glabrous at nodes. ..... *M. globuliflora* var. *globuliflora.*
        15. Branches scurfy to setose at nodes. ..... *M. globuliflora* var. *vulcanica.*
    14. Upper internodes > 2 cm long; flowers perfect; bracts much shorter than flowers; stigmata flaring.
        16. Leaves consistently 3-nerved; flowers with calyx calyptrate, rupturing irregularly, petals sparsely stellate-puberulent abaxially. ..... *M. cornifolia.*
        16. Leaves generally 5-nerved; flowers with calyx valvate, petals glabrous.
            17. Flowers sessile.
                18. Flowers secund along panicle branches. ..... *M. laevigata.*
                18. Flowers glomerulate at tips of panicle branches. ..... *M. acinodendron.*
            17. Flowers pedicellate.
                19. Leaf surfaces concolorous. ..... *M. striata.*
                19. Leaves much darker above than below. ..... *M. andersonii.*
13. Leaves entire.
    20. Leaves dark and glossy above, much lighter below.
        21. Leaves ovate to elliptic, not more than twice as long as broad; St. Lucia.
            22. Plants glabrous (occasionally sparsely stellate on petioles); flowers not secund, calyx 2.6–4 mm long, petals pink. ..... *M. luciana.*
            22. Inflorescence axes and abaxial veins stellate-puberulent; flowers secund, calyx 1.5–2.5 mm long, petals white. ..... *M. secunda.*
        21. Leaves narrowly ovate to narrowly elliptic or lanceolate, more than twice as long as broad; St. Vincent and Grenada. ..... *M. andersonii.*
    20. Leaves concolorous; plants widespread, weedy. ..... *M. laevigata.*

NAMES PUBLISHED FOR LESSER ANTILLEAN TAXA OF MICONIA AND MELASTOMA

Miconia abortiva Naudin, Ann. Sci. Nat. Bot. III, **16:** 232. 1851. TYPE: Guadeloupe, on La Soufrière, *L'Herminier s.n.* (holotype, P! (staminate)). Cogniaux (1888) referred this species to the synonymy of *M. globuliflora.*
= **Miconia globuliflora** var. **vulcanica** (Naudin) R. Howard & E. Kellogg (see below).

Miconia acinodendron (L.) Sweet, Hortus Brit. ed. 1. 159. 1826. BASIONYM: *Melastoma acinodendrum* L. Sp. Pl. **1:** 389. 1753. LECTOTYPE (here designated): Linnaeus, Hortus Cliffort. 162. 1737 (photocopy!). In the Lesser Antilles this species occurs only on Martinique. We have the following records: Antilles, Martinique, *Plée 740* (P!); near forestry post

at Donis-Balata, *Stehlé 2137* (NY!, a fragmentary collection); Grand-Rivière, crête de Balata, alt. 400–450 m, 12.iv.1980, *Sastre 6929* (P!).

Melastoma aculeata Presl, Isis (Oken) **21:** 272. 1828. Presl cited Sieber, Fl. Martin. suppl. 113, without description. = **Charianthus nodosus** (Desr.) Triana.

Melastoma acuminata Desr. *in* Lam. Encycl. Méth. Bot. **4:** 54. 9 Feb. 1797, not M. Vahl, March 1797. TYPE: Guadeloupe, *Badier 56* (holotype, P!). = **Miconia cornifolia** (Desr.) Naudin.

Melastoma acuminata M. Vahl, Eclogae Amer. **1:** 47. *t. 7.* 1797. TYPE: ex Ind. Occ. [Montserrat, *Ryan*] (holotype, C!), IDC 2201. 46: I. 5. = **Tetrazygia discolor** (L.) DC.

Miconia albicans (Sw.) Triana, Trans. Linn. Soc. London **28:** 116. 1871. BASIONYM: *Melastoma albicans* Sw. Prodr. 70. 1788. LECTOTYPE (here designated): Jamaica, *Swartz s.n.* (S!, photo at A!). Grisebach reported this from Guadeloupe but cited no specimens. He (1860, p. 256) erroneously listed *M. albicans* as a synonym of *M. holosericea* DC., stating "common in all the West Indian islands. Hab. Jamaica!, all coll., to Trinidad!." The two species are distinct, but we have seen no Lesser Antillean specimens of either at A, BM, GH, NY, P, or US. It is possible that Grisebach confused a specimen of *M. mirabilis* with *M. holosericea.*

Melastoma alpina Sw. Prodr. 71. 1788. TYPE: Guadeloupe, *Du Ponthieu s.n.* (holotype, BM, photo at A!). = **Charianthus alpinus** (Sw.) R. Howard (see Howard, 1972).

Miconia ambigua (Rich.) DC. Prodr. **3:** 189. 1828. BASIONYM: *Melastoma ambigua* Rich. *in* Bonpl. Monogr. Melast. 55. *t. 25.* 1809. TYPE: Venezuela, Caripe in prov. Cumanae, *Bonpland 368* (holotype, P!). All Lesser Antillean material so annotated is better assigned to *Miconia laevigata,* which is distinguished from true *M. ambigua* by its secund inflorescences.

Miconia andersonii Fawcett & Rendle, J. Bot. **64:** 104. 1926. TYPE: none designated. Cogniaux (1891) cited *Anderson s.n.* ("Jamaica," but probably actually St. Vincent), *Eggers 6146, pro parte, 6220b,* and *6704* (St. Vincent, Grenada). Cogniaux (1891) described *Miconia trinervia* (not *M. trinervia* (Sw.) D. Don) and cited specimens from Jamaica and the Lesser Antilles. Fawcett and Rendle (1926a) later concluded that the Lesser Antillean specimens were distinct from the rest of *M. trinervia* Cogn. and renamed them *M. andersonii.*

Melastoma angustifolia Sw. Prodr. 71. 1788. LECTOTYPE (here designated): Jamaica, *Swartz s.n.* (S!). = **Tetrazygia angustifolia** (Sw.) DC.

Miconia antiguensis Urban, Repert. Spec. Nov. Regni Veg. **17:** 162. 1920. TYPE: Antigua, near All Souls, 4–16 Feb. 1913, *Rose, Fitch, & Russell 3288* (holotype, B, destroyed; isotype, NY!). Wurdack (in litt.) suggested that *Box 727* and *Broadway 1904* may also be *M. antiguensis.* A note on *Box 1526* (BM) reads, "A portion of this specimen has been compared

with the type of *Miconia antiguensis* Urban, in New York Bot. Gard., and found to agree exactly. Harold E. Box 24/8/39." = **Miconia striata** (M. Vahl) Cogn.

Melastoma aquatica Aublet, Hist. Pl. Guiane Fr. **1:** 430. *t. 169.* 1775. TYPE: [sur la route de Caïenne à Couru,] BM, LINN-SM 654.11, IDC 5073. 302: II. 2 (photo!) (see also Howard, 1983). = **Nepsera aquatica** (Aublet) Naudin.

Miconia berbiceana (DC.) Naudin, Ann. Sci. Nat. Bot. III, **16:** 174. 1851. BASIONYM: *Clidemia berbiceana* DC. Prodr. **3:** 160. 1828. TYPE: Berbice, *Anonymous s.n.* (holotype, G-DC), IDC 800. 507: III. 7 (photo!). HOMOTYPIC SYNONYM: *Tschudya berbiceana* (DC.) Griseb. Fl. Brit. W. Indian Is. 250. 1860. This was originally described as from Guyana. Naudin cited *Plée 740,* Martinique (P!), but this is a specimen of *M. acinodendron.* Cogniaux assigned the name to the synonymy of *Miconia acinodendron* (L.) Sweet.

Melastoma brachiata M. Vahl, Eclogae Amer. **3:** 24. 1807. SYNTYPES: Montserrat, *Ryan 2 et 7* (holotype, C!), IDC 2201. 46: I. 6, 7. = **Miconia laevigata** (L.) D. Don.

Melastoma calyptrata Desr. *in* Lam. Encycl. Méth. Bot. **4:** 51. 9 Feb. 1797. TYPE: "Vahl 1797 Guadeloupe" and "vide specimen in Surian herb. 177..752," P-JU #14045, IDC 6206. 1033: II. 4 (photo!). HOMOTYPIC SYNONYM: *Melastoma calyptrata* M. Vahl, Eclogae Amer. **1:** 40. March 1797. = **Conostegia calyptrata** (Desr.) D. Don.

Miconia candolleana Naudin, Ann. Sci. Nat. Bot. III, **16:** 244. 1851, *nomen illegit.* This is a renaming of *Melastoma lutescens* M. Vahl. = **Miconia cornifolia** (Desr.) Naudin.

Miconia candolleana Triana, Trans. Linn. Soc. London **28:** 117. 1871, *nomen illegit.* This is a renaming of **Miconia cinnamomifolia** (DC.) Naudin, not *M. cinnamomifolia* (Jacq.) Triana. See discussion under *M. cinnamomifolia.* Wurdack (1960) mistakenly cited this as *M. candolleana* (DC.) Triana.

Melastoma capitata M. Vahl, Eclogae Amer. **1:** 45. 1797. TYPE: [India occidentali, Schumacher, Professor Chirurgiae Hauniensis,] Dr. Banks [ex] Dryander (holotype, C!), IDC 2201. 66: II. 6, 7. Triana (1871) placed this species in *Tristemma,* but Wickens (1975) assigned it to *Melastomastrum.* Wickens believed that the plant may have been grown at Kew by Dryander; a specimen was obtained by Schumacher and sent to Vahl, who erroneously reported it from the West Indies. = **Melastomastrum capitatum** (M. Vahl) A. & R. Fernandes, an African species.

Miconia caribaea Domin, Preslia **9:** 3, 4. 1930. TYPE: St. Vincent, Sandy Bay, *H. H. & G. W. Smith 820* (holotype, K!). = **Miconia andersonii** Fawcett & Rendle.

Miconia catalpifolia Kränzl, Vierteljahrsschr. Naturf. Ges. Zürich **76:** 153.

1931. TYPE: Dominica, 700 m, *Eggers 750* (holotype, B, destroyed; isotype, GH!). = **Graffenriedia latifolia** (Naudin) Triana.

Miconia ceanothina DC. Prodr. **3:** 189. 1828. SYNTYPES: Guadeloupe, *Perrottet s.n.* (G-DC), IDC 800. 515: I. 6–8; Cuba, *De la Ossa s.n.* (G-DC?, not seen). = **Miconia laevigata** (L.) D. Don.

Miconia christophoriana (Ham.) DC. Prodr. **3:** 200. 1828 [as *christophorianum*]. BASIONYM: *Melastoma christophoriana* Ham. Prodr. Pl. Indiae Occ. 37. 1825. TYPE: "St. Kitts, v.v." No specimen located (see Howard *et al.*, 1981). Cogniaux (1891) referred this name to **Tetrazygia discolor** (L.) DC.

Melastoma ciliata Desr. *in* Lam. Encycl. Méth. Bot. **4:** 49. 1797. TYPE: Guadeloupe, *Badier s.n.* (holotype, P, not found—no specimen in P-JU or P-LAM). = **Tibouchina ornata** (Sw.) Baillon (see Howard, 1972).

Miconia ciliata (Rich.) DC. Prodr. **3:** 179. 1828. BASIONYM: *Melastoma ciliata* Rich. Actes Soc. Hist. Nat. Paris **1:** 109. 1792. (Not Desr., 1797, which is *Tibouchina ornata* (Sw.) Baillon.) TYPE: French Guiana, *Leblond s.n.* (holotype, P!). HOMOTYPIC SYNONYM: *Miconia racemosa* var. *ciliata* Griseb. Fl. Brit. W. Indian Is. 258. 1860. Cogniaux (1891) cited an Anderson collection from St. Vincent, where it was presumably in cultivation. *Anderson 18* (BM!), labeled "Ind. Occ.," was actually collected in Surinam. Naudin (1851) listed this species as a synonym of *M. racemosa,* but Wurdack (1973) distinguished the two on the basis of leaf nervation—*M. ciliata* has three nerves, *M. racemosa* five.

Miconia cinnamomifolia (DC.) Naudin, Ann. Sci. Nat. Bot. III, **16:** 168. 1851. BASIONYM: *Cremanium cinnamomifolium* DC. Prodr. **3:** 194. 1828. TYPE: Brazil, Martius herb. #13 (*fide* Triana, 1871). HOMOTYPIC SYNONYM: *Miconia candolleana* Triana, Trans. Linn. Soc. London **28:** 117. 1871. *Miconia cinnamomifolia* (DC.) Naudin is the legitimate combination in *Miconia* of the epithet *cinnamomifolia* (see below).

Miconia cinnamomifolia (Jacq.) Triana, Trans. Linn. Soc. London **28:** 101. 1871, *nomen illegit.* BASIONYM: *Melastoma cinnamomifolia* Jacq. Collect. **2:** 111. *t. 6, fig. 2.* 1788. TYPE: [Martinica,] Jacquin's plate. This is an illegitimate transfer of the epithet into *Miconia.* = **Miconia cornifolia** (Desr.) Naudin.

Melastoma coccinea Rich. Actes Soc. Hist. Nat. Paris **1:** 109. 1792. TYPE: Guadeloupe, *Richard s.n.* (holotype, P!). = *Charianthus coccineus* (Rich.) D. Don = **Charianthus alpinus** (Sw.) R. Howard (see Howard, 1972).

Melastoma coccinea M. Vahl, Eclogae Amer. **1:** 48. 1797. TYPE: Montserrat, *Ryan s.n.* (holotype, C!), IDC 2201. 46: II. 5, 6. = **Charianthus purpureus** D. Don.

Melastoma compressa M. Vahl, Eclogae Amer. **3:** 23. 1807. (Not *Miconia compressa* Naudin, a Brazilian species.) TYPE: "in Caribeis," *Rohr s.n.* (holotype, C, not seen). = **Miconia mirabilis** (Aublet) L. O. Williams.

Miconia coriacea (Sw.) DC. Prodr. **3:** 189. 1828. BASIONYM: *Melastoma coriacea* Sw. Prodr. 70. 1788. TYPE: Ind. Occid., *Swartz s.n.* (holotype, BM, not found; isotype, s!). Although Swartz noted in his initial description that this species was to be found on Montserrat, he did not repeat the mention of Montserrat in his later publication (1800). Instead, he cited the Soufrière on Guadeloupe and indicated that a specimen was in the Banks Herbarium (BM). We were unable to find the specimen there. We have seen specimens only from Guadeloupe and Dominica; reports from Montserrat and Martinique may be erroneous, referring to the similar *M. globuliflora* and its varieties.

Melastoma cornifolia var. *grandifolia* Rich. *in* Bonpl. Monogr. Melast. 94. 1812. TYPE: Martinique, [*Bonpland s.n.*] (holotype, P!). = **Miconia cornifolia** (Desr.) Naudin.

Melastoma cornifolia var. *parvifolia* Rich. *in* Bonpl. Monogr. Melast. 94. 1812. TYPE: Martinique, *Bonpland s.n.* (holotype, P!). = **Miconia cornifolia** (Desr.) Naudin.

Miconia cornifolia (Desr.) Naudin, Ann. Sci. Nat. Bot. III, **16:** 126. 1851. BASIONYM: *Melastoma cornifolia* Desr. *in* Lam. Encycl. Méth. Bot. **4:** 51. 1797. TYPE: in the general collection at P is a specimen labeled "e martinica no. L61," with "Lamk. scrips" in the corner of the label. We presume this to be the holotype. HOMOTYPIC SYNONYMS: *Conostegia cornifolia* (Desr.) Ser. ex DC. Prodr. **3:** 175. 1828. *Tetrazygia cornifolia* (Desr.) Griseb. Fl. Brit. W. Indian Is. 255. late 1860 (almost simultaneously published in Goett. Abh. **9:** 53. 14 Dec. 1860). The calyx of this species is frequently calyptrate, explaining its placement in *Tetrazygia* and *Conostegia*.

Melastoma corymbosa Rich. Actes Soc. Hist. Nat. Paris **1:** 109. 1792. TYPE: Guadeloupe, *Richard s.n.* (holotype, P!). = **Charianthus corymbosus** (Rich.) Cogn.

Melastoma corymbosa M. Vahl, Eclogae Amer. **3:** 25. 1807. TYPE: Martinique, *Rohr 168* (holotype, C!), IDC 2201. 46: II. 7, III. 1. = **Charianthus corymbosus** (Rich.) Cogn.

Melastoma crinita M. Vahl, Eclogae Amer. **3:** 28. 1807. TYPE: Martinique, no collection cited. = **Charianthus nodosus** (Desr.) Triana (*fide* Cogniaux, 1891).

Melastoma cymbifolia Rich. *in* Bonpl. Monogr. Melast. 57. *t. 26.* 1809, *nomen illegit.* TYPE: Sulphurariae Guadlupensis, *Richard s.n.* (holotype, P! (in fruit)). This is a renaming of *Melastoma coriacea.* = **Miconia coriacea** (Sw.) DC.

Melastoma decussata M. Vahl, Eclogae Amer. **1:** 42. 1797, *nomen illegit.* SYNTYPES: *Rohr 119* (C!), IDC 2201. 46: III. 4, 5; *Ryan* [&] *Rohr* ex Cajenna N. *119* (C!). This is a renaming of *Melastoma racemosa* Aublet. = **Miconia racemosa** (Aublet) DC.

Melastoma discolor L. Syst. Nat. ed. 10. **2:** 1022. 1759. LECTOTYPE (here designated): Sloane, Voy. Jamaica **2:** *t. 198, fig. 1.* 1725. *Miconia discolor* DC. is from Brazil and is not the same species. = **Tetrazygia discolor** (L.) DC.

Melastoma dodandiana Ham. Prodr. Pl. Indiae Occ. 37. 1825. TYPE: "Dodand (St. Kitts), Nevis, v.v." No specimen found (see Howard *et al.,* 1981). = **Charianthus purpureus** D. Don.

Miconia dodecandra (Desr.) Cogn. *in* C. Martius, Fl. Brasil. **14**(4): 243. 1887. BASIONYM: *Melastoma dodecandra* Desr. *in* Lam. Encycl. Méth. Bot. **4:** 46. 1797. TYPE: "*Clarck,*" herb. D. Thouin (holotype, P, not found; isotype, MPA). The name *Miconia dodecandra* has been applied to plants with abundant pubescence on the calyx and mature fruit; *M. mirabilis* includes only plants with glabrous fruits. There are two specimens in the general collection at P, both labeled *M. dodecandra* but with glabrous calyces: *no. L63* (in Lamarck's handwriting), "habitat in Martinica," "?leg. Joseph Martin" (written in pencil, apparently at a later date); and *Herb. Surian 56* (hb. Jussieu?). Lamarck cited these in the protologue, commenting, "Les fruits paroissent glabres"; they should probably be regarded as paratypes. The Clarck specimen may have been sent by T. Clarke, superintendent of the botanical garden in Jamaica, and seems not to have had fruits. Lamarck described the calyx as having a "duvet incane," but this would be consistent with a representative of either *M. dodecandra* or *M. mirabilis.* It is possible that *M. dodecandra* should in fact be placed in the synonymy of *M. mirabilis,* and what has been called *M. dodecandra* renamed, but this should probably wait until the Clarke material is located.

Melastoma eleagnoides Sw. Prodr. 72. 1788 [as *aeleagnoides*], not Cogn. TYPE: Ind. occid., hb. Casströmii (lectotype, here designated, BM; isolectotype, S!). = **Tetrazygia eleagnoides** (Sw.) DC.

Melastoma elegans Aublet, Hist. Pl. Guiane Fr. **1:** 427. *t. 167.* 1775. TYPE: [Caienne,] BM, LINN-SM 782.31, IDC 5073. 347: III. 4 (photo!) (see Howard, 1983). = **Clidemia hirta** (L.) Don var. **elegans** (Aublet) Griseb.

Miconia elongata Vahl ex Stehlé & Quentin, Fl. Guad. Dépend. **2**(3): 91. 1949, not Cogn. ex Britton (a Bolivian species). BASIONYM: *Melastoma elongata* M. Vahl, Eclogae Amer. **3:** 16. 1807. TYPE: Montserrat, *Ryan 6* (holotype, C!), IDC 2201. 47: I. 1, 2. Stehlé and Quentin listed *Melastoma elongata* M. Vahl and *Miconia semicrenata* Naudin under "*Miconia elongata* (ubi?)," indicating that they had not found the combination published. They cited the Antillean distribution as Montserrat, Dominica, St. Vincent, Grenada, Grenadines, Guadeloupe, and Martinique. *Melastoma elongata* M. Vahl is an illegitimate renaming of *Melastoma acuminata* Desr. = **Miconia cornifolia** (Desr.) Naudin.

Miconia ernstii Wurd. Phytologia **11:** 385. 1965. TYPE: Dominica, on south

slope of Morne Macaque (Micotrin) on the road to Fresh Water Lake, elev. ca. 760 m, *W. R. Ernst 1723* (holotype, US!).

Melastoma expansa M. Vahl, Eclogae Amer. **3:** 21. 1807. TYPE: Montserrat, *Ryan s.n.* (holotype, C!; isotype, BM!), IDC 2201. 47: I. 3, 4. = **Miconia laevigata** (L.) D. Don.

Melastoma farinulentum Sw. ex Wikström, Kongl. Svenska Vetenskapsakad. Handl. **1827:** 65. 1828. TYPE: Guadeloupe, *Forsström s.n.* ex herb. Casströmii (holotype, S, photo at A!). Although the protologue says "floribus. . .decandris," the flowers of the type specimen have only four anthers. = **Miconia tetrandra** (Sw.) D. Don.

Miconia florida (DC.) Naudin, Ann. Sci. Nat. Bot. III, **16:** 244. 1851. BASIONYM: *Diplochita florida* DC. Prodr. **3:** 176. 1851. TYPE: Cayenne, *R. Delniart s.n.* (holotype, G-DC), IDC 800. 511: III. 8 (photo!). = **Miconia mirabilis** (Aublet) L. O. Williams.

Melastoma fothergilla Bonpl. var. *lanceolata* Bonpl. Monogr. Melast. 71. 1809. This variety is based on *Fothergilla mirabilis* Aublet (see above). = **Miconia mirabilis** (Aublet) L. O. Williams.

Miconia fothergilla Naudin, Ann. Sci. Nat. Bot. III, **16:** 119. 1851. SYNONYMS: *Melastoma fothergilla* Bonpl. Monogr. Melast. 71. *t. 32.* 1809, *nomen illegit.* This is a renaming of *Fothergilla mirabilis* Aublet. *Diplochita fothergilla* (Bonpl.) DC. Prodr. **3:** 176. 1828. = **Miconia mirabilis** (Aublet) L. O. Williams.

Miconia furfuracea (M. Vahl) Griseb. Fl. Brit. W. Indian Is. 257. late 1860 (almost simultaneously published in Goett. Abh. **9:** 54. 14 Dec. 1860). BASIONYM: *Melastoma furfuracea* M. Vahl, Eclogae Amer. **3:** 13. *t. 22.* 1807. TYPE: [India occidentalis,] *Ziegler s.n.* (holotype, C!), IDC 2201. 47: I. 5, 6. Vahl's Ic. Ill. Pl. Amer. 3. *t. 22.* 1799 is also *M. furfuracea.*

Miconia globulifera (Rich.) Cham. ex Triana *sensu* Stehlé & Quentin, Fl. Guad. Dépend. **2**(3): 85. 1949, not Naudin. = **Miconia globuliflora** (Rich.) Cogn.

Miconia globuliflora (Rich.) Cogn. *in* C. Martius, Fl. Brasil. **14**(4): 418. 1888. BASIONYM: *Melastoma globuliflora* Rich. Actes Soc. Nat. Hist. Paris **1:** 109. 1792. TYPE: Guyane-française (probably actually from Martinique), *Leblond s.n.* (G-DC). At P! there is a specimen in hb. Richard labeled *Melastoma globuliflora* "in Martinicae."

Richard described *Melastoma globuliflora* based on a Leblond collection bearing the printed label "Guyane-française—M. Leblond, 1792." Cogniaux (1891) and others have accepted this record, but Wurdack (1972) has indicated that other collections from South America labeled with this name represent doubtful records. Leblond went to Martinique in 1767 and visited other islands in the West Indies and countries in northern South America. His collections were returned to Europe and

reported by Richard (Lasègue, 1845). It is possible that the printed label is in error.

Schlechtendal and Chamisso (1830) described "*Melastoma* (?) *globuliflorum*" from Mexico based on the Schiede and Dieppe collection (photo seen). Naudin (1851) described *Miconia globulifera,* citing *Melastoma globuliferum* Schldl. & Cham. By our present rules, if Naudin was transferring the Schlechtendal and Chamisso species to *Miconia,* he made an error in spelling; however, the Schlechtendal and Chamisso name was a later homonym so the Mexican species is properly renamed as *Miconia globulifera* Naudin. For the Antillean material, Cogniaux (1888, 1891) used the name *Miconia globuliflora* (Cham. ex Triana) Cogn. but cited *Melastoma globuliflora* Rich. in synonymy. The name is properly *Miconia globuliflora* (Rich.) Cogn.

This species is part of a complex of dioecious miconias, the members of which are distinguished from each other primarily by pubescence distribution. *Miconia globuliflora* var. *globuliflora* is entirely glabrous or has a slightly scurfy area near the distal end of the petiole; we have seen specimens from Nevis, Montserrat, Martinique, and St. Lucia. (Some St. Lucia specimens have setae along the internodes but not clustered at the nodes.) The type of *Melastoma thyrsoidea* M. Vahl is also included in this group. A second group of plants, most common on Dominica but also found on St. Kitts and Nevis, is characterized by tufts of long setae at the nodes; we describe this below as *Miconia globuliflora* var. *dominicae* R. Howard & E. Kellogg. A third group is endemic to Guadeloupe and has both tufted-setose nodes and additional long setae at the distal end of the petiole and the base of the blade; these plants have been known as *M. vulcanica* Naudin, but we reduce them to the rank of variety under *M. globuliflora. Miconia coriacea* is closely related to the *M. globuliflora* complex, but we maintain it as a distinct species on the basis of its thicker stems, dense pubescence on most internodes, revolute leaf margins, and ascending leaves.

Miconia globuliflora var. **dominicae** R. Howard & E. Kellogg, var. nov.

Frutex vel arbor, caulis internodiis quadrangularis, minus quam 5 mm longis, nodiis setis caespitosis. Folii grandi, 6.5–18 cm longi, glabri. Petioli glabri. Flores unisexuales, plantae dioeciae. Bracteae oblanceolatae, longiores quam flores. Antherae biporosae. Stigmata capitata. Varietas differt a M. globuliflora var. globuliflora nodiis setis caespitosis petiolisque glabris et foliis grandioribus.

Dioecious shrub or small tree to 6 m tall; branching sympodial, with axis terminated by inflorescence, the axillary branch immediately below elongating simultaneously with flowering; branches more or less quadrangular when young, internodes often only 5 mm long; nodes scurfy or with tufts of colleters up to 4.5 mm long. Leaves with petiole 10–50 mm long, dark, glabrous; blade ovate, elliptic, or oblong, 6.5–18 × 3–9 cm, glabrous, the apex acuminate, the base cuneate to rounded, the margin with incurved dentations, the nerves 5 from base, with 3 inner

ones more prominent. Inflorescence a terminal panicle; flowers unisexual; bracts oblanceolate, cucullate, early caducous, those immediately below flowers surpassing perianth, lower ones commensurately larger; calyx 1.7–2.5 mm long, glabrous, with 5 broadly deltate teeth; petals 5, white, blade ovate to orbicular; stamens with the anthers ca. 1 mm long, flaring distally, abruptly truncate at 2 large pores, sometimes developed on pistillate plants but then empty, the filaments enlarged below, linear above; style 2.2–3 mm long, stigma capitate. Fruits 3.5–5 mm in diameter, dark blue.

TYPE. Dominica, Morne Trois Pitons, mossy forest at summit, altitude 763–1400 m, 23 Feb. 1946, *Hodge 1398* (holotype, GH!; isotype, BM!).

SPECIMENS SEEN. **Dominica:** Morne Trois Pitons, alt. 1200 m, *Beard 631* (NY), *Fishlock s.n.*, 1915 (NY); St. George Parish, above 2000 ft, E of Laudat on road to Freshwater Lake, *Gillis 8212* (GH); Morne Trois Pitons, rainforests on upper slopes, alt. 763–1400 m, *Hodge 1406* (GH); Morne Anglais, upper mossy forest-clad slopes, alt. 763–1142 m, *Hodge 2307* (GH); Morne Plat Pays, mossy forest on summit, altitude 981 m, *Hodge & Hodge 1676* (GH); rainforest borders between Laudat and Freshwater Lake, alt. ca. 665 m, *Hodge & Hodge 1750* (GH); Morne Diablotin, mossy forests on N ridges, alt. ca. 1300 m, *Hodge & Hodge 2814* (GH (2 sheets)); vic. Fresh Water Lake, near Laudat, alt. 450–600 m, *A. C. Smith 10254* (A), *10297* (A); forested slopes of Micotrin along trail from point ca. ½ mi beyond Laudat to one ca. ½ mi beyond Fresh Water Lake (L'étang), alt. 2300–2700 ft, *Wilbur 7387* (GH). **Nevis.** Nevis Peak: summit, alt. 3596 ft, *Proctor 19320* (A), *19334* (A, BM); S slope, alt. 300–600 m, *A. C. Smith 10518* (A). **St. Kitts:** vic. Dodans Pond, Verchild's Mtn., alt. ca. 2750 ft, *Proctor 19588* (A); E spur of Mt. Misery, alt. 1500–2500 ft, *Proctor 19609* (A, BM). **Montserrat:** summit of Chance's Mtn., alt. 2700 ft, *Howard & Howard 17527* (A), alt. 2800–3000 ft, *Proctor 19111* (BM); slopes of Chance's Mtn., *Howard & Howard 19714* (A); summit of English Peak, alt. 2600 ft, *Howard & Howard 15207* (A). **Trinidad(?):** without further locality, *Sieber 128* (BM).

Miconia globuliflora (Rich.) Cogn. var. **vulcanica** (Naudin) R. Howard & E. Kellogg, comb. nov. BASIONYM: *Miconia vulcanica* Naudin, Ann. Sci. Nat. Bot. III, **16:** 213. 1851. TYPE: Guadeloupe, *Funck & Schlim s.n.* (holotype, P! (staminate)). *Miconia vulcanica* and *Miconia abortiva* were both described from unisexual and incomplete material. Both types were collected on the Soufrière of Guadeloupe and represent one species. For more discussion of this variety, see *M. globuliflora.*

Melastoma grossularioides L. Sp. Pl. **1:** 390. 1753. TYPE: none at LINN.
= **Bellucia grossularioides** (L.) Triana.

Miconia guianensis (Aublet) Cogn. Jahrb. Königl. Bot. Gart. Berlin **4:** 280. 1886. BASIONYM: *Tamonea guianensis* Aublet, Hist. Pl. Guiane Fr. **1:** 441. 1775. TYPE: BM, not seen. Louis Williams (1963) concluded that the correct name for this species is **Miconia mirabilis,** the name used in most copies of Aublet's *Histoire des Plantes de la Guiane françoise* (see also Howard, 1983, and Zarucchi, 1984).

Miconia guianensis (Aublet) Cogn. var. *ovalis* Cogn. *in* C. Martius, Fl. Brasil.

14(4): 246. 1887. TYPE: Martinique, *Richard s.n.* (holotype, P, photo at A!). SYNONYM: *Melastoma fothergilla* Bonpl. var. *ovalis* Bonpl. Monogr. Melast. 71. 1809, *nomen illegit.* (a renaming of *Melastoma dodecandra* Lam. and *M. compressa* M. Vahl). = **Miconia mirabilis** (Aublet) L. O. Williams.

Miconia guianensis (Aublet) Cogn. var. *vulgaris* Cogn. *in* C. Martius, Fl. Brasil. **14**(4): 246. 1887. This is the typical variety of *M. guianensis* (Aublet) Cogn. = **Miconia mirabilis** (Aublet) L. O. Williams.

Miconia herbiceana Naudin, *Clidemia herbiceana* DC., and *Tschudya herbiceana* Griseb. cited in Fournet (1978) as synonyms of **Miconia acinodendron.** This is a misspelling of *berbiceana.*

Melastoma hirta L. Sp. Pl. **1:** 390. 1753. TYPE: "America meridionali," LINN 559.2 (559.3 also labeled *C. hirta* but inflorescence terminal). = **Clidemia hirta** (L.) D. Don.

Melastoma holosericea M. Vahl, Eclogae Amer. **1:** 42. 1797, not L., 1753, Sw., 1791, or Triana, 1871. TYPE: ex Cayenne, [*Rohr*] (holotype, C!), IDC 2201. 47: I. 7. = **Miconia albicans** (Sw.) Triana.

Melastoma icosandrum Sw. *in* Wikström, Kongl. Svenska Vetenskapsakad. Handl. **1827:** 64. 1828. LECTOTYPE (here designated): Guadeloupe, *Forsström s.n.* (S!). = **Conostegia icosandra** (Sw.) Urban.

Miconia impetiolaris (Sw.) D. Don ex DC. Prodr. **3:** 183. 1828. BASIONYM: *Melastoma impetiolaris* Sw. Prodr. 70. 1788. LECTOTYPE (here designated): Ind. Occ., *Swartz s.n.* (S!). HOMOTYPIC SYNONYM: *Acinodendron impetiolare* (Sw.) Kuntze, Rev. Gen. Pl. **1:** 244. 1891.

Miconia lacera (Rich.) Naudin, Ann. Sci. Nat. Bot. III, **16:** 152. 1851. BASIONYM: *Melastoma lacera* Rich. *in* Bonpl. Monogr. Melast. 9. *t. 5.* 1807. TYPE: Nouvelle Grenada, Mariquita, *Richard s.n.* (holotype, P #5758!). HOMOTYPIC SYNONYM: *Clidemia lacera* DC. Prodr. **3:** 164. 1828. Neither Richard nor De Candolle cited any Lesser Antillean specimens. Naudin cited a Plée specimen, probably *Plée 610* from Martinique (P!). Also reported (by Cogniaux, 1891) was *Sieber 468,* which we were unable to find at P. In addition, there is an Anderson specimen at BM! incorrectly labeled "Ind. Occ." This is a Colombian species and was most likely cultivated.

Melastoma laevigata Aublet, Hist. Pl. Guiane Fr. **1:** 412. *t. 159.* 1775, not L., 1759. SYNTYPES: Guyane (hb. Barbier, P!); BM, LINN-SM 782.30, IDC 5073. 347: I. 4 (photo!); P-JU #14109 (photo at A!) (see Howard, 1983). = **Miconia prasina** (Sw.) DC.

Miconia laevigata (L.) D. Don *in* Sweet, Hortus Brit. 159. 1826, not DC., 1828. BASIONYM: *Melastoma laevigata* L. Syst. Nat. ed. 10. **2:** 1022. 1759. LECTOTYPE: LINN 559.10. HOMOTYPIC SYNONYM: *Acinodendron laevigatum* (L.) Kuntze, Rev. Gen. Pl. **1:** 244. 1891. Fawcett & Rendle (1926) noted that the Sloane reference cited in synonymy by Linnaeus

refers to a specimen of *Zizyphus chloroxylon.* Rendle designated as lectotype a Browne specimen in the Linnaean herbarium labeled *M. laevigata* by Linnaeus, apparently LINN 559.10. LINN 559.9 is another Browne specimen of the same species but "bears the epithets 'parviflora' (crossed out by Linnaeus) and 'discolor' in Linnaeus' hand. The sheet also bears the letters 'C' and 'Br.' 'Discolor' has been crossed out, but by Smith who suggests that it is really *laevigata.* This is because 'C' is correlated with *M. laevigata* L. in *Syst. nat.* ed. 10 and because the specimen conflicts with Linnaeus' diagnosis for *discolor* by *not* having, 'margine laevibus'" (C. E. Jarvis, in litt.). The bibliographic citation is often incorrectly published as *Miconia laevigata* (Desr.) DC. De Candolle did indeed cite only the Lamarck reference, but Desrousseaux credited Linnaeus without specific reference.

Miconia lambertiana DC. Prodr. **3:** 185. 1828. TYPE: St. Vincent, 1816, *M. Lambert s.n.* (holotype, G-DC), IDC 800. 514: I. 3 (photo!). Cogniaux referred this plant to *Miconia longifolia* (Aublet) DC. Lambert was never in St. Vincent; his specimens from the island were sent to him by Anderson. Presumably the plant was cultivated, but we have seen no specimens other than the type.

Miconia lanata (DC.) Triana, Trans. Linn. Soc. London **28:** 113. 1871. BASIONYM: *Clidemia lanata* DC. Prodr. **3:** 162. 1828. SYNTYPES: Guiana, 1816, *M. Lambert s.n.* (G-DC), IDC 800. 508: II. 8 (photo!); Cuba, Havana, 1825, *Ossa s.n.* (G-DC), IDC 800. 508: II. 6 (photo!); Trinidad, *Sieber 66* (G-DC), IDC 800. 508: II. 7 (photo!). HOMOTYPIC SYNONYMS: *Tschudya lanata* (DC.) Griseb. Fl. Brit. W. Indian Is. 250. 1860. *Melastoma lanata* Lambert herb. ex DC. Prodr. **3:** 162. 1828. *Staphidium lanata* (DC.) Naudin, Ann. Sci. Nat. Bot. III, **17:** 324. 1852. There is a specimen (K) from the Forsyth Herbarium attributed to Anderson from Guiana. Gleason (1932, p. 180) stated, "There is a single sheet of this species from Guiana collected by Anderson. Since it is known to occur in the island of St. Vincent, where Anderson collected, it is possible that the specimen may come from there instead." Cogniaux (1887–1888) also attributed the plant to St. Vincent ("Anderson, Guilding, Caley"), and to Puerto Rico on the basis of a Bertero collection. It has not been found again in Puerto Rico or St. Vincent, and these records are presumably of former cultivation. There is also a specimen at G-DC (*M. Lambert s.n.,* 1816; IDC 800. 508: II. 5 (photo!)) from St. Vincent.

Miconia lanceolata (Desr.) DC. Prodr. **3:** 190. 1828. BASIONYM: *Melastoma lanceolata* Desr. *in* Lam. Encycl. Méth. Bot. **4:** 43. 1797. TYPE: S. Domingue, *Martin s.n.* (holotype, P-JU #14040), IDC 6206. 1033: I. 5 (photo!). Triana (1871) reported this "in insula Dominica (Martin, Beauvois)," apparently a transcriptional error, since he also cited Naudin (1851, p. 202), who had recorded the range as "in insula *Saint-Domingue*: Martin, Beauvois." The species is native to Hispaniola and does not occur in the Lesser Antilles.

Melastoma lateriflora M. Vahl, Eclogae Amer. **1:** 48. 1797. TYPE: Montserrat, *Ryan 8* (holotype, C!), IDC 2201. 47: II. 1, 2. = **Henriettea lateriflora** (M. Vahl) R. Howard & E. Kellogg, comb. nov. We concur with Williams (1963) that *Henriettella* and *Henriettea* are best combined under the name *Henriettea.*

Melastoma latifolia Desr. *in* Lam. Encycl. Méth. Bot. **4:** 31. 1797, not Naudin, 1851. TYPE: Antilles (holotype, P-JU #14073), IDC 6206. 1034: III. 7 (photo!), 1035: I. 1 (photo!). = *Clidemia latifolia* (Desr.) DC. = **Clidemia umbrosa** (Sw.) Cogn.

Miconia longifolia (Aublet) DC. Prodr. **3:** 184. 1828. BASIONYM: *Melastoma longifolia* Aublet, Hist. Pl. Guiane Fr. **1:** 432. *t. 170.* 1775. TYPE: BM, LINN-SM 782.16, IDC 5073. 347: I. 3 (photo!) (see Howard, 1983). HOMOTYPIC SYNONYM: *Chaenopleura longifolia* (Aublet) Griseb. Fl. Brit. W. Indian Is. 260. late 1860 (almost simultaneously published in Goett. Abh. **9:** 55. 14 Dec. 1860). Cogniaux (1887–1888) recognized this species from South America (Brazil, French Guiana, Surinam, Colombia) and Trinidad; he also cited an Anderson specimen from St. Vincent. Cogniaux placed *Miconia lambertiana* in the synonymy of *M. longifolia*; De Candolle described *M. lambertiana* from St. Vincent, citing a Lambert specimen. None of these specimens was found at P. This was presumably once cultivated.

Miconia luciana H. A. Gleason, J. Arnold Arbor. **28:** 334. 15 July 1947 (almost simultaneously published in Caribbean Forest **8:** 105. 1947). TYPE: St. Lucia, Quilesse, alt. 300 m, *J. S. Beard 477* (holotype, NY, photo at A!; isotypes, A!, K!).

Melastoma lutescens M. Vahl, Eclogae Amer. **3:** 17. 1807, not Bonpl., 1809 (a plant from Peru). TYPE: Montserrat, *Ryan s.n.* (holotype, C!), IDC 2201. 47: II. 3, 4. De Candolle (1828) referred this species to *Conostegia lutescens* ("Ser." ms.) DC., citing *Melastoma lutescens* M. Vahl, Eclogae Amer. **3:** 17. = **Miconia cornifolia** (Desr.) Naudin.

Melastoma macrophylla Desr. *in* Lam. Encycl. Méth. Bot. **4:** 44. 1797, not Steudel, 1844. TYPE: Hispaniola, *Martin s.n.* (holotype, P, not seen). = **Miconia impetiolaris** (Sw.) D. Don ex DC. (*fide* Urban, Symb. Antill. **8:** 493. 1921).

Miconia martinicensis Cogn. *in* DC. Monogr. Phanerog. **7:** 913. 1891. TYPE: Martinique, *Hahn 1174* (lectotype (here designated), P!; isolectotype, K!). Cogniaux cited three syntypes, *Hahn 838, Hahn 1174,* and *Duss s.n.* The Duss collection has not been located. The protologue cites *Hahn 838,* but the specimens of this species at P and elsewhere are labeled *858*; presumably the number in the protologue is a typographical error. *Hahn 858* (BM!, K!, P!) is in flower and would be preferable as a lectotype, but because the number contradicts the protologue, we have chosen *Hahn 1174,* a fruiting collection. Although Sastre has annotated the specimens at P as *Miconia coriacea* DC., he now believes (and we concur)

that *M. martinicensis* is a distinct species, distinguished by its terete, glabrous branches.

Melastoma matuba Sprengel, Neue Entd. **3:** 61. 1822. TYPE: "Guadalupa et Antigua" (holotype, B, presumed destroyed). De Candolle (1828) listed this as an unplaced species. Triana (1871) referred it to *Miconia trichotoma.*

Miconia mirabilis (Aublet) L. O. Williams, Fieldiana, Bot. **29:** 574. 1963. BASIONYM: *Fothergilla mirabilis* Aublet, Hist. Pl. Guiane Fr. **1:** 441. *t. 175.* 1775. TYPE: "Caienne," *Aublet s.n.* in hb. Poiret (BM, LINN-SM 782.51 (IDC 5073. 348: III. 3 (photo!)), P!). HOMOTYPIC SYNONYM: *Tamonea guianensis* Aublet, Hist. Pl. Guiane Fr. **1:** 441, in some copies. Williams has pointed out that various copies of Aublet's work use the name *Fothergilla mirabilis* or *Tamonea guianensis* with the description.

Melastoma montana Sw. Prodr. 69. 1788. TYPE: Jamaica, *Swartz s.n.* (holotype, BM, not seen; specimens at S are labeled "Ind. Occ." and "Guadeloupe"). = **Conostegia montana** (Sw.) D. Don.

Miconia myricoides (Desr.) DC. Prodr. **3:** 202. 1828. BASIONYM: *Melastoma myricoides* Desr. *in* Lam. Encycl. Méth. Bot. **4:** 51. 1797. TYPE: Antilles, *Surian 733* (holotype, P, not seen). Triana (1871) placed in the synonymy of this species *Miconia thyrsoidea* (M. Vahl) DC., *M. sieberi* DC., non Griseb., *M. abortiva* Naudin, and "*M. globuliflora* Cham." = **Miconia globuliflora** (Rich.) Cogn. var. **globuliflora.**

Melastoma nigricans M. Vahl, Eclogae Amer. **3:** 26. 1807; Ic. Ill. Pl. Amer. 3. *t. 27.* 1799, *nomen illegit.* TYPE: *Rohr 167* (holotype, C! (IDC 2201. 47: II. 5, 6); isotype, BM!). This is a renaming of *Melastoma trichotoma* Desr. = **Miconia trichotoma** (Desr.) DC.

Melastoma nodosa Desr. *in* Lam. Encycl. Méth. Bot. **4:** 55. 1797. TYPE: *Surian 93* (holotype, P, not seen). = **Charianthus nodosus** (Desr.) Triana.

Melastoma ornata Sw. Prodr. 69. 1788. TYPE: Jamaica, *Swartz s.n.* (holotype, BM; isotype, S, not seen). = **Tibouchina ornata** (Sw.) Baillon (see Howard, 1972).

Melastoma pallens Sprengel, Neue Entd. **3:** 62. 1822. TYPE: Hispaniola (holotype, B, presumed destroyed). Cogniaux (1891) reported this species from Dominica based on a Schomburgk collection; this is an error for the Dominican Republic. = **Tetrazygia pallens** (Sprengel) Cogn.

Miconia parviflora (Aublet) Cogn. *in* DC. Monogr. Phanerog. **7:** 805. 1891. BASIONYM: *Melastoma parviflora* Aublet, Hist. Pl. Guiane Fr. **1:** 433. *t. 171.* 1775. TYPE: BM, LINN-SM 782.13 (IDC 5073. 346: III. 7 (photo!)) (see Howard, 1983). *Miconia parviflora* Macfad. (Fl. Jamaica **2:** 90. 1837. TYPE: Jamaica, *Wharton s.n.,* not seen) makes illegitimate Cogniaux's transfer of this epithet to *Miconia.* Cogniaux (1887) also published *Miconia parviflora* (Bentham) Cogn., utilizing as a basionym *Diplochita*

parviflora Bentham (TYPE: British Guiana, *Schomburgk 483*, K). Gleason (1932) accepted this name, but Wurdack (1973) has correctly designated the northern South American species as *Miconia pubipetala* Miq. = **Miconia prasina** (Sw.) DC.

Melastoma pendulifolia Rich. Actes Soc. Hist. Nat. Paris **1:** 109. 1792. TYPE: see discussion. Triana (1871) added this name to the synonymy of *Miconia prasina* (Sw.) DC. The type should be from Guyana. There is a specimen at P in herb. Richard, referable to *M. prasina*, but the location is given as "in sylvulis ridivivis Guadl.," the same citation as for *Melastoma pendulifolia* Bonpl. (1809); however, the illustration for the latter species appears to be a specimen of *M. laevigata* (L.) DC. and is certainly not *M. prasina*. Triana (1871) placed *M. pendulifolia* Bonpl. in the synonymy of *M. laevigata*. Either *M. pendulifolia* Bonpl. is illustrated by a specimen that is not the type and is properly typified by the Richard specimen, or the type specimen has not been found and the species should be lectotypified on the illustration. The specimen from Guadeloupe is probably not the type of *M. pendulifolia* Rich., although no other candidate for the type has been found.

Miconia pendulifolia DC. Prodr. **3:** 187. 1828. TYPE: Bonpland's plate may be the best type for this species, unless a specimen can be found (see above). SYNONYM: *Melastoma pendulifolia* Bonpl. Monogr. Melast. 79. *t. 35.* 1809, *nomen illegit.* = **Miconia laevigata** (L.) D. Don.

Miconia picta Wurd. Phytologia **7:** 235. 1960. SYNTYPES: Montserrat, *Ryan 3* (C!), IDC 2201. 47: III. 4, 5; *Ryan s.n.* (C!). SYNONYM: *Melastoma picta* M. Vahl, Eclogae Amer. **3:** 15. 1807, *nomen illegit.* This is a renaming of *Melastoma cornifolia* Desr. = **Miconia cornifolia** (Desr.) Naudin.

Melastoma pilosa Sw. Prodr. 72. 1788. TYPE: Jamaica, *Swartz s.n.* (holotype, S, not seen). = **Clidemia guadalupensis** Griseb.

Melastoma piluliferum M. Vahl, Eclogae Amer. **3:** 15. 1807. TYPE: Martinique, *Rohr 102* (holotype, C!). = **Miconia laevigata** (L.) DC.

Miconia prasina (Sw.) DC. Prodr. **3:** 188. 1828. BASIONYM: *Melastoma prasina* Sw. Prodr. 69. 1788. LECTOTYPE (here designated): Jamaica, *Swartz s.n.* (S!). HOMOTYPIC SYNONYM: *Acinodendron prasinum* (Sw.) Kuntze, Rev. Gen. Pl. **1:** 245. 1891. Swartz (1800) cited *Melastoma laevigata* Aublet, Hist. Pl. Guiane Fr. **1:** 171, 443. 1775, but this is not *Melastoma laevigata* L. Fawcett and Rendle (1926b) referred to Swartz specimens from Hispaniola (BM!) and Jamaica (S!) without designating a lectotype.

Miconia pteropoda Bentham, J. Bot. (Hooker) **2:** 314. 1840, not Naudin, 1851. TYPE: British Guiana, *Schomburgk s.n.* (holotype, K). Urban (1921) cited the distribution to include Guadeloupe and Grenada. No specimens have been seen from outside northern South America. Specimens at K (*Broadway 5898*, Grenada; and *Grisebach s.n.*, Guadeloupe) are labeled *M. pteropoda* but are really *M. prasina*. According to Wurdack (1973), *M. pteropoda* = **Miconia prasina** var. **crispula** Cogn.

Melastoma pulverulentum Sw. ex Wikström, *nomen nudum.* Cogniaux (1891) cited this as being published in "Sw. ex Wikstr. Guadel. Fl. 64; Linnaea, V, Lit.-Ber. 90," but it is not in either place.

Melastoma punctulatum Sw. *in* Wikström, Kongl. Svenska Vetenskapsakad. Handl. **1827:** 65. 1828. TYPE: "in Guadalupa," *Forsström s.n.* (s, not seen). = **Charianthus alpinus** (Sw.) Howard.

Miconia purpuracea (M. Vahl) Griseb. ex Stehlé & Quentin, Fl. Guad. Dépend. **2**(3): 87. 1949. This is a misspelling of the epithet of *Melastoma furfuracea* M. Vahl.

Melastoma purpurascens Aublet, Hist. Pl. Guiane Fr. **1:** 402. *t. 154.* 1775. TYPE: BM, LINN-SM 782.38, IDC 5073. 348: I. 4 (photo!) (see Howard, 1983). = **Aciotis purpurascens** (Aublet) Triana.

Miconia pyramidalis (Desr.) DC. Prodr. **3:** 188. 1828. BASIONYM: *Melastoma pyramidalis* Desr. *in* Lam. Encycl. Méth. Bot. **4:** 53. 1797 ("communiquée par M. Badier"). TYPE: Guadeloupe, 1787, *Badier s.n.* (holotype, P-JU #14094!; isotype, A!). = **Miconia laevigata** (L.) D. Don.

Miconia pyramidalis (Desr.) DC. var. *ciliolata* DC. Prodr. **3:** 188. 1828. Based on *Melastoma portoricense* Sprengel, Neue Entd. **3:** 61. 1822. TYPE: [Puerto Rico] (holotype, B, presumed destroyed). When he reduced Sprengel's species to varietal rank, De Candolle extended the range to include Guadeloupe and Trinidad. = **Miconia laevigata** (L.) D. Don, *fide* Urban, Symb. Antill. **4:** 457. 1910.

Miconia racemosa (Aublet) DC. Prodr. **3:** 179. 1828. BASIONYM: *Melastoma racemosa* Aublet, Hist. Pl. Guiane Fr. **1:** 406. *t. 156.* 1775. TYPE: no specimen was cited by Lanjouw & Uittien (1940) for the Aublet Herbarium, and none was found at P, but Howard (1983) cited BM; LINN-SM 782.4, IDC 5073. 346: II. 5 (photo!); P-JU #14085, IDC 6206. 1035: III. 3, 4 (photo!). HOMOTYPIC SYNONYM: *Acinodendron racemosum* (Aublet) Kuntze, Rev. Gen. Pl. **1:** 245. 1891.

Miconia racemosa DC. var. *barbigera* (DC.) Cogn. *in* C. Martius, Fl. Brasil. **14**(4): 411. 1888. BASIONYM: *Miconia barbigera* DC. Prodr. **3:** 179. 1828. TYPE: Cayenne, *Patris s.n.* (holotype, G-DC, photo at A!), IDC 800. 512: III. 3. Cogniaux (1891) cited *Eggers 6053* from Grenada. Triana (1871) placed this in the synonymy of *Miconia decussata,* which is **Miconia racemosa** (Aublet) DC.

Miconia rivoeriae Naudin, Ann. Sci. Nat. Bot. III, **16:** 170. 1851. SYNTYPES: Martinique, *Rivoire s.n.* (GH!, P!); Guadeloupe, *L'Herminier s.n.* (P!). SYNONYM: *Cremanium rivoeriae* (Naudin) Griseb. Fl. Brit. W. Indian Is. 262. 1860. = **Miconia trichotoma** (Desr.) DC.

Miconia rubens (Sw.) Naudin, Ann. Sci. Nat. Bot. III, **16:** 169. 1851. BASIONYM: *Melastoma rubens* Sw. Prodr. 71. 1788. LECTOTYPE (here designated): Jamaica, *Swartz s.n.* (S!). SYNONYM: *Cremanium rubens* Griseb. Fl. Brit. W. Indian Is. 261. 1860. *Miconia rubens* (Sw.) Naudin was considered

endemic to Jamaica by Adams (1972). However, Wurdack (1973) also reported it from Venezuela, and Gleason (1958) recorded it for Costa Rica and Panama. Grisebach cited this species from Guadeloupe, presumably on the basis of his accepted synonym of *Miconia abortiva* Naudin, which is *Miconia globuliflora* (Rich.) Cogn. var. *vulcanica* (Naudin) R. Howard & E. Kellogg.

Melastoma rubra Aublet, Hist. Pl. Guiane Fr. **1**: 416. *t. 161.* 1775. TYPE: BM, LINN-SM 782.34, IDC 5073. 347: III. 7 (photo!) (see also Howard, 1983). The only record from the Lesser Antilles is *Proctor 16951* from Grenada. = **Clidemia rubra** (Aublet) C. Martius.

Miconia secunda R. Howard & E. Kellogg, sp. nov.

Frutex vel arbor parva, foliis ovatis vel ellipticis, basi cordatis vel rotundatis, quinquinervis, praeter venas abaxiales glabris. Rami inflorescentiarum cincinnati, floribus secundis, sessilis. Antherae uniporatae, 1.2–2 mm. Stigmata expansa. Species differt a Miconia trichotoma floribus secundis.

Small tree or shrub, 5–12 m tall; young branches compressed, tetragonal, appressed stellate-furfuraceous as are petioles, inflorescence axes, bracts, and calyces. Leaves with petiole (9–)14–54 mm long; blade ovate to elliptic, 10.5–27 × 4.9–16.2 cm, the apex short-acuminate, the base cuneate, rounded, or cordate, the margin entire, the nerves 5, basal or inner 2 suprabasal, with 2 intramarginal ones weaker than other 3, the leaf surfaces glabrous except primary abaxial veins stellate-furfuraceous. Inflorescences panicles, 10–21.5 cm long, ultimate branches cincinnate; flowers sessile, secund, scented; bracts lanceolate below to deltate or broadly ovate above, decreasing in size acropetally from 1.5 to 3 mm long. Calyx conical, 1.5–2.5 mm long, stellate-pubescent, obscurely 5-crenate, ca. upper half free from ovary, forming hypanthium; petals oblong-oblanceolate, clavate, 1.3–2 mm long, white; anthers flaring, truncate, 1.2–2 mm long, uniporate, extended basally to 2 minute appendages; pistil with the style linear, 2.3–4.7 mm long, glabrous, the stigma more or less flaring, papillate. Berry 3.5–3.9 mm in diameter, pink, becoming black, 10-ribbed when dry.

TYPE. St. Lucia, Savanne Edmund district, southeast of Piton Troumasse, elev. 1800–2000 ft, 22, 23 April 1958, *Proctor 17726* (holotype, A; isotype, BM).

SPECIMENS SEEN. **St. Lucia:** Barre de l'Îsle, Castries–Dennery Road, alt. 350–400 m, *Cowan 1559* (GH, P), *1575* (GH, P); La Sorcière, Castries Waterworks Reserve, alt. 280 m, *Rollet HUC 1324* (A); Castries Waterworks Reserve along track E at Forestière pump station, alt. 950 ft, slope 10%, exposure N, clayey forest loam, *Slane 228* (A).

Wurdack (1965) had noted that this was probably a new species.

Miconia semicrenata (Rich.) D. Don *in* Loudon, Hortus Brit. **1**: 174. 1830. BASIONYM: *Melastoma semicrenata* Rich. *in* Bonpl. Monogr. Melast. 69. *t. 31.* 1809. TYPE: Guadeloupe, *Richard s.n.* (holotype, P!). HOMOTYPIC

SYNONYMS: *Conostegia semicrenata* Ser. ex DC. Prodr. **3:** 175. 1828. *Tetrazygia semicrenata* Griseb. Fl. Brit. W. Indian Is. 255. late 1860 (almost simultaneously published in Mem. Amer. Acad. Arts **8:** 185. Dec. 1860). D. Don also listed *Miconia semicrenata* in Sweet, Hortus Brit. 159. 1826, but the place of origin is merely "W. Indies" and there is no other diagnostic information. Don (*in* Loudon, 1830) listed the origin as Guadeloupe, suggesting that he was referring to Richard's species. = **Miconia cornifolia** (Desr.) Naudin.

Melastoma septemnervium Jacq. Select. Stirp. Amer. Hist. 131. 1763. TYPE: "habitat in sylvis montosis Martinicae." Jacquin's description is not diagnostic, there is no illustration, and no type has been found.

Melastoma sessiliflora M. Vahl, Eclogae Amer. **1:** 49. 1797. TYPE: *Rohr 130* (holotype, C!), IDC 2201. 48: I. 1, 2. = **Clidemia rubra** (Aublet) C. Martius.

Miconia sieberi DC. Prodr. **3:** 189. 1828. TYPE: Martinique (recorded as Trinidad), *Sieber 260* (holotype, G-DC, IDC 800. 515: II. 2 (photo!); isotype, BM, photo at A!). HOMOTYPIC SYNONYM: *Cremanium sieberi* (DC.) Griseb. Fl. Brit. W. Indian Is. 262. 1860. Cogniaux (1887–1888) assigned this species to the synonymy of *Miconia globuliflora* (Rich.) Cogn. Robert Williams (1934) indicated that it had not been re-collected in Trinidad. The Sieber collection is more likely from Martinique. Grisebach placed *M. vulcanica* in the synonymy of *Cremanium sieberi* and recorded it from Dominica and Guadeloupe. The microfiche photo (Prodr. Herb. 800. 515: II. 2) shows leaves 5 × 2.7 cm and apparently glabrous, characteristic of *M. globuliflora* var. *globuliflora* and not *M. globuliflora* var. *vulcanica.* = **Miconia globuliflora** (Rich.) Cogn. var. **globuliflora.**

Miconia striata (M. Vahl) Cogn. *in* DC. Monogr. Phanerog. **7:** 756. 1891. BASIONYM: *Melastoma striata* M. Vahl, Eclogae Amer. **3:** 14. 1807. TYPE: Montserrat, *Ryan 5* (holotype, C!), IDC 2201. 48: I. 3, 4. This species has been misinterpreted by Cogniaux and most recent workers to include many other species as synonyms. The distinctive pubescent calyx with small outer teeth and the glabrous petals exclude both *Miconia semicrenata* and *M. cornifolia,* included by others.

Miconia striata (M. Vahl) Cogn. var. *vincentina* Domin, Preslia **9:** 4. 1930. TYPE: St. Vincent, *H. H. & G. W. Smith 724* (holotype, K!). = **Miconia cornifolia** (Desr.) Naudin.

Melastoma tamonea Sw. Prodr. 70. 1788, *nomen illegit.* This is a renaming of *Tamonea guianensis* Aublet. = **Miconia mirabilis** (Aublet) L. O. Williams.

Miconia tetrandra (Sw.) D. Don *in* Sweet, Hortus Brit. 159. 1826. BASIONYM: *Melastoma tetrandra* Sw. Prodr. 72. 1788. TYPE: Jamaica, *Swartz s.n.* (lectotype, S!, photo at A!; isolectotypes, BM!, C!). HOMOTYPIC SYNONYMS: *Tetrazygia tetrandra* (Sw.) DC. Prodr. **3:** 172. 1828. *Cremanium te-*

trandrum (Sw.) Griseb. Mem. Amer. Acad. Arts **8:** 166. 1861. Although D. Don did not cite Swartz as the author of the epithet, he listed the place of origin as Jamaica and the date of introduction as 1815, information that is repeated in Loudon (1830), along with a reference to Swartz.

Miconia theaezans (Bonpl.) Cogn. *in* C. Martius, Fl. Brasil. **14**(4): 419. 1888. BASIONYM: *Melastoma theaezans* Bonpl. Monogr. Melast. 17. *t. 9.* 1807. TYPE: Colombia, Popayán, *Bonpland s.n.* (holotype, P, not seen). A Masson specimen determined as this species and supposedly collected on St. Kitts is at BM (photo at A!). The specimen may actually be a representative of *Miconia globuliflora* var. *dominicae. Miconia theaezans* is otherwise unknown from the Lesser Antilles. Triana (1871) placed this species in the synonymy of *M. milleflora* Naudin.

Miconia thyrsiflora (D. Don) Naudin, Ann. Sci. Nat. Bot. III, **16:** 244. 1851. BASIONYM: *Cremanium thyrsiflorum* D. Don, Mem. Wern. Nat. Hist. Soc. **4:** 312. 1823. TYPE: Peru, *Pavon s.n.* (holotype, G-BOISS; isotype, OXF). This species is Peruvian and has nothing to do with the Caribbean species *Melastoma thyrsoidea* M. Vahl, but the names have been confused by some authors. Naudin (1851, p. 244) could not place this species but referred it to *Miconia* as "*Miconia thyrsoidea,*" citing "*Cremanium thyrsoideum* Don" and DC. Prodr. **3:** 191. 1828, where the species is also called *C. thyrsoideum* Don. Wurdack (1971) believed that Naudin should be credited with the combination. Cogniaux (1891, p. 934) used *Miconia thyrsoidea,* attributing a "nomen" to Naudin. Cogniaux did not see the Pavon specimen. He listed *Cremanium thyrsoideum* D. Don in synonymy, perpetuating Naudin's error, and also *Miconia thyrsiflora* Triana, in which the correct combination was made. Macbride's treatment of *Miconia* for the Flora of Peru (1941) used *Miconia thyrsoidea* (Don) Naudin, noting that the species had not been re-collected and the locality was to be questioned. An F negative (29507) was cited. At GH there is a photograph of a Pavon specimen in Berlin (*Gleason 7-2*) considered a type collection; Wurdack (1971) assigned this to *Miconia nitida* (D. Don) Naudin.

Melastoma thyrsoidea M. Vahl, Eclogae Amer. **3:** 13. 1807. TYPE: Montserrat, *Ryan 9* (holotype, C!), IDC 2201. 48: I. 5, 6. Not *Miconia thyrsoidea* (D. Don) Cogn., which is *Miconia thyrsiflora* (see above). = **Miconia globuliflora** (Rich.) Cogn. var. **globuliflora.**

Miconia trichotoma (Desr.) DC. Prodr. **3:** 188. 1828. BASIONYM: *Melastoma trichotoma* Desr. *in* Lam. Encycl. Méth. Bot. **4:** 53. 1797. TYPE: Antilles, Herbier de Surian (holotype, P-JU #14084!).

Melastoma triflora M. Vahl, Eclogae Amer. **1:** 46. 1797, not Naudin, 1851 (a species from Goa, India, that may need a new name). TYPE: Caribeis, *Forseith s.n.* (holotype, C!), IDC 2201. 48: I. 7, II. 1. De Candolle (1828) listed this as an unplaced species. = **Henriettea triflora** (M. Vahl) Alain.

Miconia trinervia (Sw.) D. Don *in* Loudon, Hortus Brit. 174. 1830. BASIONYM: *Melastoma trinervia* Sw. Prodr. 69. 1788. LECTOTYPE (here designated): Jamaica, *Swartz s.n.* (s!). In transferring this epithet to *Miconia,* Don cited *Melastoma trinervis* Willd., an error for *M. trinervia* Willd. Willde- now cited Swartz. Although Don listed *Miconia trinervia* in Sweet (1826), no country of origin is listed and the date of introduction does not agree with that in Loudon (1830); the identity of the plant is therefore not certain. Cogniaux (1891), not having seen Swartz's original specimen, used this name for a second species, represented by specimens from St. Vincent and Grenada. Fawcett and Rendle renamed the species represented by these specimens *Miconia andersonii.* Two Anderson specimens at BM labeled *Miconia trinervia* are *M. andersonii.*

Melastoma umbrosa Sw. Prodr. 72. 1788, not Cogn. TYPE: St. Christopher, hb. Alstroemer (lectotype, BM; isolectotype, s!). SYNONYM: *Sagraea umbrosa* DC. Prodr. **3:** 171. 1828. = **Clidemia umbrosa** (Sw.) Cogn.

Melastoma verticillata M. Vahl, Eclogae Amer. **1:** 47. 1797, *nomen illegit.,* not Triana, 1871 (a Brazilian species). TYPE: Caribeis, "*Forseith*" *s.n.* (holotype, C!). Most species in Forsyth's herbarium were sent to him from St. Vincent by Anderson. = *Clidemia verticillata* (M. Vahl) DC. = **Clidemia guadalupensis** (DC.) Griseb.

Miconia virescens (M. Vahl) Triana, Trans. Linn. Soc. London **28:** 107. 1871. BASIONYM: *Melastoma virescens* M. Vahl, Eclogae Amer. **3:** 18. 1807. SYNTYPES: ex Trinidad, *Ryan, Rohr s.n.* (C!); ex Ins. Trinitatis, *Rohr s.n.* (C!), IDC 2201. 48: II. 2, 3. Louis Williams (1963) suggested that this species is synonymous with *Miconia laevigata* (L.) DC. Stehlé, Stehlé, and Quentin (1949) recognized the species in Guadeloupe as having flowers with a smaller calyx than those of *Miconia laevigata.* We have found that variation in calyx length is continuous and therefore follow Williams. = **Miconia laevigata** (L.) D. Don.

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NOTES ON SIMPLE-LEAVED CHINESE SPECIES OF SORBUS (ROSACEAE) FROM HUBEI PROVINCE

STEPHEN A. SPONGBERG[1]

Eight species of simple-leaved *Sorbus* L. (Maloideae, Rosaceae) have been attributed to the flora of Hubei Province in the People's Republic of China (Yü & Lu, 1974; Anonymous, 1979). Of these, six were reported from the Shennongjia Forest District in western Hubei by the 1980 Sino-American Botanical Expedition (Bartholomew *et al.*, 1983). The determinations listed in the expedition report were based on comparisons of materials in the herbarium of the Institute of Botany, Academia Sinica, Beijing, and in the combined collections of the Arnold Arboretum and the Gray Herbarium. However, further study of the expedition materials, as part of a broader revisionary study of the simple-leaved species of *Sorbus* in all of eastern and southeastern Asia and the Himalayan region, has revealed that a previously undescribed new species is represented in the collections made during the 1980 expedition. In addition, examination of the type specimens that pertain to the names of the simple-leaved Hubei species has clarified one nomenclatural problem in the group.

In proposing the new species, I take great pleasure naming it in honor of Professor Te-tsun Yü, former director of the Beijing Botanical Garden and vice director, Institute of Botany, Academia Sinica, foremost student of Asiatic *Sorbus*, and a primary advocate of renewed and continued cooperation between Chinese and American botanists.

Sorbus yuana Spongberg, sp. nov. FIGURE 1.

Sorbus zahlbruckneri sensu auct., not Schneider; Yü, Fl. Reip. Pop. Sin. **36:** 292. *pl. 40, figs. 13–15.* 1974; Gabrielian, Genus Sorbus W. Asia Himalayas, 183. 1978, with regard to the citation of *W. Y. Chun* [*R. C. Ching*] *4230.*

Species Sorbus zahlbruckneri affinis, sed foliis latioribus (3.2–9.4 versus 2.9–4.7 cm latis, maxime 1.7- versus minime 2.3-plo longioribus quam latioribus), marginibus profunde necnon regulatim duplicato-serratis, et fructibus grandioribus (10–16 × 6–13 versus 6–8 × 4–5 mm), differt.

Small to medium-sized trees to ca. 15 m tall, d.b.h. to ca. 25 cm, sometimes branching into 2 or 3 trunks near base; bark gray; buds ovoid, 9–12 mm long, to ca. 4 mm broad at base, with 2 short outer scales and 4 inner imbricate ones, the scales chestnut-brown, ± glaucous, sometimes with scattered whitish hairs along margins, otherwise glabrous; branchlets ± stout, reddish brown,

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becoming purplish or gray-black with small, elongate or rounded lenticels in second and third years. Leaves with petioles 1.3–2.7 cm long, downy with floccose pubescence to ± glabrous, sulcate along adaxial surface, with groove ± closed along its length; stipules not seen; blades 6–12.7 cm long, 3.2–9.4 cm wide (length/width quotient 1.2–1.7), elliptic to broadly ovate, the bases subcordate, rounded, obtuse, or cuneate, the apices acute to short-acuminate, the margins recurved, deeply and regularly double-serrate, the upper surfaces dark green (often drying brown), glabrous, with midvein and secondary veins impressed and colleters lacking, the lower surfaces pale green, glabrous or having sericeous pubescence along veins, with midvein and 11 to 13 pairs of secondary veins prominently elevated, secondary veins arising at 40–50° angles and terminating in serrations of double-serrate margin, tertiary veins not regularly interconnecting adjacent secondary veins. Inflorescences and flowers not seen. Infructescences large, widely branched, compound corymbs to 20 cm across terminating elongated shoots, the primary and secondary branches ± stout, terete or slightly flattened and angled, purplish brown, heavily lenticellate, glabrous or with areas of weblike, floccose pubescence. Fruits 10–16 mm long, 6–13 mm wide, ovate to characteristically obovate, cherry-red (and sweet) at maturity (dull purplish red when dried), the surface smooth, glaucous, with few scattered lenticels and areas of floccose pubescence (particularly at often ± oblique base and at apex), the apex with persistent withered remains of calyx, stamens, and densely white-pubescent style base; ovary 2-locular, each with 2 ovules, 1 or both often abortive, the nonabortive ones developing into obovate seeds ca. 7 mm long, 4 mm wide, with testa dark reddish brown.

TYPE. People's Republic of China, Hubei Province, Shennongjia Forest District (31°30′N, 110°30′E), between Yinpo and Qiaodonggou Canyon on the road between Jiuhuping Forest Farm and Bancang, elevation ca. 2100 m, 19 Sept. 1980, *1980 Sino-American Bot. Exped. 1555* (holotype, A; isotypes, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH,[2] UC, WH).

ADDITIONAL SPECIMENS EXAMINED. **People's Republic of China.** HUBEI: Giu Fu Ping, 2130 m alt., *W. Y. Chun* [*R. C. Ching*] *4230* (A); Shennongjia Forest Distr., Hong-ping Xiang-ja-cao, 2000 m alt., *Shennongjia Botany Investigation Team 32270* (HIB); Shennongjia Forest Distr., Tian-men-bar, 2000 m alt., *Shennongjia Botany Investigation Team 32687* (HIB, 2 sheets); Shennongjia Forest Distr., Jiou-hu-ling Chang, Pao-zi Gou, *Anonymous 34032* (HIB, 2 sheets); Shennongjia Forest Distr., just S of Tianmen Pass, ca. 2300 m alt., *1980 Sino-American Bot. Exped. 1728* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); Xingshan Xian, Xingshan, *Anonymous 811* (HIB).

DISTRIBUTION AND ECOLOGY. Known only from western Hubei Province in the Shennongjia Forest District and neighboring Xingshan Xian at or above 2000 m alt. Rare tree of steep ravine slopes. Seeds of *Sorbus yuana* were introduced by the 1980 Sino-American Botanical Expedition into the United States, and living plants raised from that introduction are to be expected in the collections of arboreta and botanical gardens.

According to Yü and Kuan's (1963) and Yü and Lu's (1974) infrageneric division of the simple-leaved Chinese species of *Sorbus*, *S. yuana* falls into

[2]Shennongjia Forest District Herbarium.

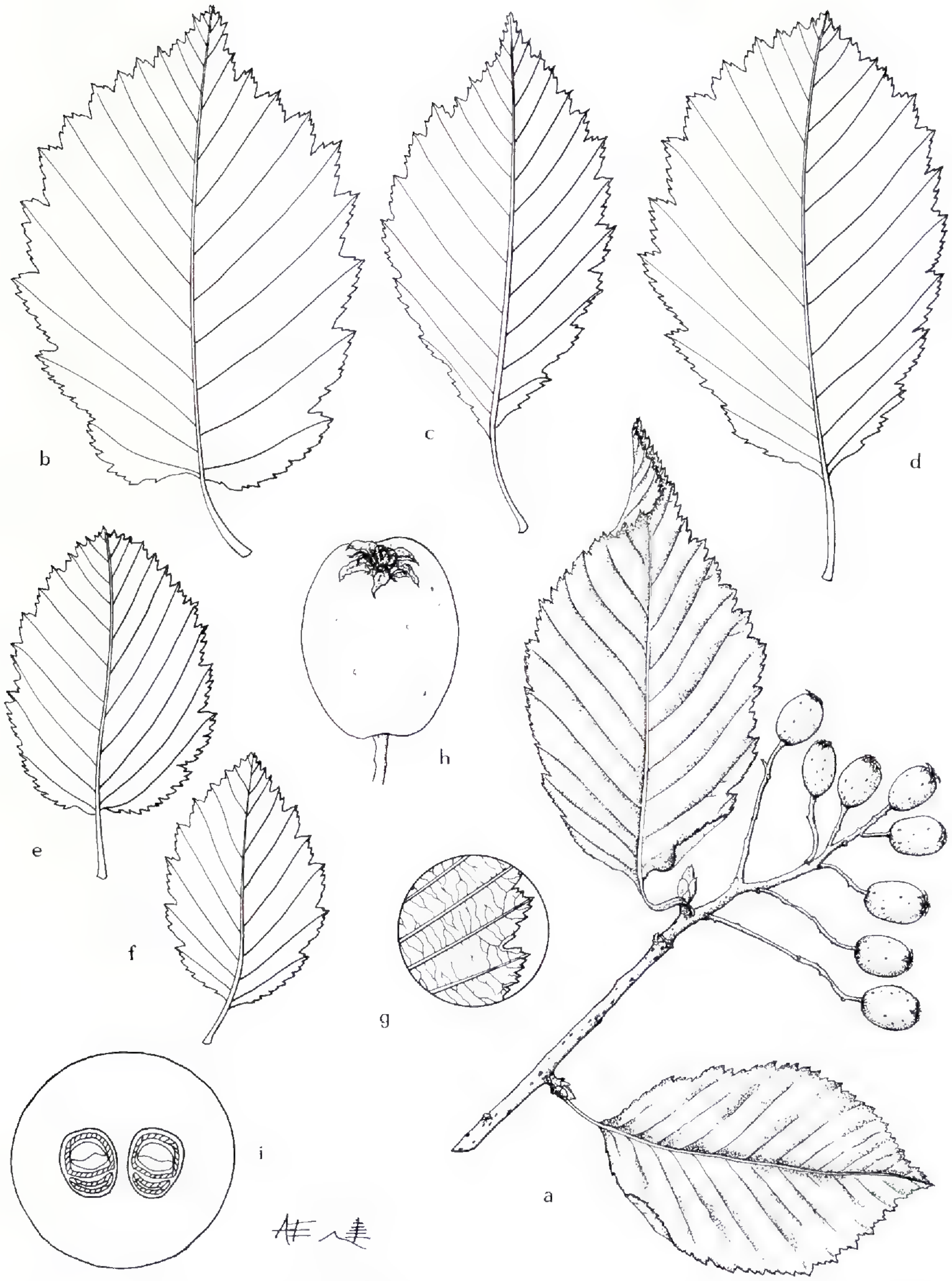

FIGURE 1. **Sorbus yuana:** a, habit of fruiting branchlet, × 0.5; b–f, outlines of leaves, all × 0.5; g, detail of leaf venation and margin, × 0.75, showing tertiary veins interconnecting lateral veins; h, fruit with persistent sepal lobes and anther filaments, × 1.5; i, cross section of fruit, × 2.

ser. *Thibeticae* Yü of sect. *Aria* Pers. Represented by two additional species in the Hubei flora, ser. *Thibeticae* includes *S. hemsleyi* (Schneider) Rehder, from western Hubei and Sichuan, and *S. zahlbruckneri* Schneider, from western Hubei and eastern Sichuan. Most specimens of *S. yuana* have previously been

associated with *S. zahlbruckneri,* which has been a poorly understood species of very limited distribution. In fact, the two collections of *S. yuana* made by the 1980 Sino-American Botanical Expedition were initially identified as *S. zahlbruckneri.* These three species can be distinguished from one another utilizing the following key; because flowering material of *S. yuana* has not been seen, only vegetative and fruit characters are used.

KEY TO THE HUBEI SPECIES OF SORBUS, SERIES THIBETICAE

1. Upper surfaces of leaves lacking colleters along midveins; fruits 2-locular, ovoid or obovoid, sparingly lenticellate, red at maturity.
   2. Leaves 6–12.7 cm long, 3.2–9.4 cm wide, length/width quotient < 1.7, margins deeply and regularly double-serrate; fruits 10–16 mm long, 6–13 mm in diameter. ..... *Sorbus yuana.*
   2. Leaves 8.1–11.5 cm long, 2.9–4.7(–5.4) cm wide, length/width quotient > 2.3, margins irregularly serrate to regularly but shallowly double-serrate; fruits 6–8 mm long, 4–5 mm in diameter. ..... *Sorbus zahlbruckneri.*
1. Upper surfaces of leaves with colleters scattered along midveins; fruits 3- or 4-locular, globose to depressed-globose, heavily lenticellate, greenish brown at maturity. .... *Sorbus hemsleyi.*

Although *Sorbus yuana* is extremely closely allied to *S. zahlbruckneri,* it is also very near to *S. japonica* Hedlund, a species endemic to but widely distributed on the Japanese islands of Honshu, Shikoku, Kyushu, and Yakushima (Horikawa, 1976). This relationship provides an example of a species pair linking the flora of western Hubei with that of Japan and reinforces the hypothesis of Ying, Ma, and Chang (1979) that the western Hubei flora has greater floristic affinities with the Japanese than with the Himalayan flora.

Confusion has also centered around the identity of *Sorbus hemsleyi.* This arose originally from Schneider's placement of the species in the sometimes-segregated genus *Micromeles* Decne., a seemingly arbitrary group based on a single character—the deciduous nature of the calyx lobes and associated stamens at the apex of the mature fruit. Schneider founded his species on a Henry collection (*6830A*) from Hubei, and Rehder (1915) made the combination necessary for its inclusion in *Sorbus.* Since that time, *S. hemsleyi* has been maintained as a valid species of *Sorbus* in the Chinese flora (Anonymous, 1979; Yü & Lu, 1974; Gabrielian, 1978) most often associated (Yü & Kuan, 1963; Yü & Lu, 1974; Gabrielian, 1978) with *S. folgneri* (Schneider) Rehder, another species originally described in *Micromeles.*

At the same time that Rehder provided the necessary combination for *Micromeles hemsleyi* in *Sorbus,* he also described *S. xanthoneura* as a new species from Hubei, and several specimens collected by the 1980 Sino-American Expedition have been identified as that species. Rehder based his new taxon on *Henry 6830* and allied it with *S. cuspidata* (Spach) Hedlund and *S. pallescens* Rehder, both of which belong to section *Aria* within the genus. During the present investigation, type specimens of both *S. hemsleyi* and *S. xanthoneura* have been examined and compared, and it has become obvious that both represent the same taxon. The specimen of *Henry 6830A* at Kew was annotated by Schneider and dated 13 May 1906; it is considered to be the holotype of

S. hemsleyi. Moreover, the fact that *S. xanthoneura* is a synonym of *S. hemsleyi* was recognized by T. T. Yü as early as 1950, as his annotation label on the Kew sheet attests. As a result, the following synonymy can be provided for *S. hemsleyi*.

Sorbus hemsleyi (Schneider) Rehder, Pl. Wilsonianae **2:** 276. 1915.

Micromeles hemsleyi Schneider, Ill. Handb. Laubh. **1:** 704. *figs. 388a, 389c.* 1906; Repert. Spec. Nov. Regni Veg. **3:** 152. 1906. TYPE: China, Prov. Hupeh, *A. Henry 6830A* (holotype, K!; isotype, E!).

Sorbus xanthoneura Rehder, Pl. Wilsonianae **2:** 272. 1915. TYPE: China, Prov. Hupeh, *A. Henry 6830* (holotype, A!; isotypes, BM!, GH!, P!).

Pirus xanthoneura (Rehder) Cardot, Notul. Syst. (Paris) **3:** 349. 1918; Bull. Mus. Hist. Nat. (Paris) **24:** 79. 1918.

The descriptions of *Sorbus hemsleyi* published in *Flora Hupehensis* (Anonymous, 1979) and *Flora Reipublicae Popularis Sinicae* (Yü & Lu, 1974) have apparently been based on specimens representing plants of *S. folgneri* with almost spherical, more lenticellate fruits and leaves with the veins and vein axils on the lower surfaces essentially glabrous. To determine whether or not this phase is worthy of taxonomic recognition will require additional study.

Although the reduction of *Sorbus xanthoneura* to the synonymy of *S. hemsleyi* reduces the number of simple-leaved species of *Sorbus* in Hubei by one, the recognition of *S. yuana* brings the total number for this floristically rich Chinese province back to eight. Based on the recent discovery of *S. yuana*, further investigations in western Hubei may well reveal additional new species.

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FURTHER NOTES ON TURBINA AND MERREMIA: TYPIFICATION AND TAXONOMY OF THE NEOTROPICAL CONVOLVULACEAE

D. F. AUSTIN[1] AND G. W. STAPLES[2]

In 1983 we published a short paper effecting nomenclatural changes in the genera *Merremia* Dennst., *Operculina* Silva Manso, and *Turbina* Raf. Since that time one of us (G.W.S.) has examined additional specimens that necessitate some changes in the typification we proposed for the South American *Turbina cordata.* Furthermore, we are able to name the taxon described briefly as *Merremia* species A.

TURBINA

The typification of *Turbina cordata* is a complex matter for several reasons, as discussed in our previous paper (Austin & Staples, 1983). We thought we had resolved the problem satisfactorily by designating a Martius collection at the Conservatoire et Jardin Botanique, Geneva, as the lectotype for our new combination. A careful search during the summer of 1984 of the various herbaria conserved there failed to turn up the relevant specimen, and we were forced to reconsider our choice of lectotype. Additional material, long misidentified, subsequently came to light in the collections at Harvard, and some of these specimens proved to be types as well. We herewith emend our lectotypification for this taxon.

Turbina cordata (Choisy) Austin & Staples, J. Arnold Arbor. **64:** 488. 1983.

Rivea cordata Choisy *in* DC. Prodr. **9:** 326. 1845. TYPES: Brazil, Minas Gerais, in sylvis catingas ad fluv. St. Francisco prope Salgado, *Martius s.n.* [86] (lectotype, M!, photos at A, FAU), *Pohl s.n.* (syntype, M!, photos at A, FAU), *Pohl s.n.* [113] (isosyntype, G!, 2 sheets in Delessert herb.), *Pohl s.n.* [1378] (isosyntype, GH!, ex M).

Ipomoea martii Meisner *in* Martius, Fl. Brasil. 7: 258. 1869. TYPES: *Pohl* collections, as above; Brazil, Goias, *Burchell 6868* (isosyntype, GH!).

In creating the new name *Ipomoea martii* for Choisy's taxon, Meisner cited the Martius collection in the Munich herbarium, along with specimens from Warming (*s.n.*), Pohl (*s.n.*), Claussen (*288*), and Burchell (*6868*); these are all syntypes of the new name. Meisner specifically excluded the Martius specimen in Martius's own herbarium, referring it to *Ipomoea tubata* Nees.

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The Pohl collections cited above as syntypes of *Rivea cordata* are without collector's number, although two bear numbers added later that may be herbarium or catalog numbers. All of the Pohl sheets are morphologically identical, and we consider them to be duplicates of one collection.

MERREMIA

Among the material we examined in the collections of the Conservatoire et Jardin Botanique, Geneva, was the holotype of Hans Hallier's *Operculina pavoni,* a taxon we have never been able to place satisfactorily. This taxon is identical with two fragmentary specimens at the Field Museum, the basis for our *Merremia* species A. A new combination is needed.

Merremia pavonii (H. Hallier) Austin & Staples, comb. nov.

Operculina pavoni H. Hallier, Bot. Jahrb. Syst. **16:** 550. 1893. TYPE: Nova Hispania, *Pavon s.n.* [354] (G!, Boissier herb., photos at A, FAU).

The origin of the holotype specimen is obscure, and we are not convinced that this collection came from the Andes. Ruiz and Pavon collected in Peru and Chile, but their herbarium also incorporated material obtained from other collectors, including Sessé and Mociño, who worked in Mexico. Morphologically, *Merremia pavonii* is nearest to the species complex consisting of *M. platyphylla, M. palmeri,* and *M. aurea,* which range through southwestern Mexico and the southern Baja peninsula. No Andean species familiar to us is as similar to *M. pavonii* as this Mexican group is, which leads us to suspect that the holotype originated in Mexico. It should be noted, however, that among the arborescent members of *Ipomoea,* morphologically similar species are known from Mexico and the Andes (McPherson, 1981). This allows for the possibility of a parallel situation in *Merremia.* Additional collections of this species are needed to clarify the situation.

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THE GENERA OF LEPIDIEAE (CRUCIFERAE; BRASSICACEAE) IN THE SOUTHEASTERN UNITED STATES[1,2]

IHSAN A. AL-SHEHBAZ[3]

Tribe **Lepidieae** A. P. de Candolle, Syst. Nat. **2:** 151. 1821.

Annual, biennial, or perennial herbs [sometimes subshrubs or shrubs], glabrous or with simple or rarely stellate [or bifurcate or dendritic] trichomes. Inflorescence an ebracteate [or bracteate], corymbose raceme, usually elongated in fruit; flowers few to many [rarely solitary on long scapes], actinomorphic or slightly [to strongly] zygomorphic, perfect [or very rarely imperfect and plants monoecious or dioecious]. Sepals erect to ascending or spreading, not saccate [or strongly saccate] at base. Petals present or absent, equal or unequal. Nectar glands 2, 4, or 6, distinct or connate, subtending [or surrounding] the bases of

[1]Prepared for the Generic Flora of the Southeastern United States, a long-term project made possible by grants from the National Science Foundation and currently supported by BSR-8415769 (C. E. Wood, Jr., principal investigator), under which this research was completed, and BSR-8415637 (N. G. Miller, principal investigator). This account, the 111th in the series, was begun under BSR-8111520 (C. E. Wood, Jr., principal investigator). It follows the format established in the first paper (Jour. Arnold Arb. **39:** 296–346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets [ ]. The references that I have not verified are marked with asterisks.

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The illustrations were made by Karen Stoutsenberger under earlier grants. Carroll Wood and/or Kenneth R. Robertson prepared the material and supervised the illustrations. Fresh material was contributed by Wood, and the fruits and seeds are from herbarium specimens in the Gray Herbarium or the Arnold Arboretum.

[2]For an account of the family and its tribes, see Al-Shehbaz, The tribes of Cruciferae (Brassicaceae) in the southeastern United States. Jour. Arnold Arb. **65:** 343–373. 1984.

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filaments. Stamens 2 or 6 [rarely 4 or 8–24], subequal or tetradynamous, with or without a basal appendage. Siliques usually less than 3 times [very rarely to 20 times] longer than broad, strongly [to slightly] flattened at right angles to the septum (angustiseptate) [or rarely inflated], dehiscent or indehiscent [sometimes modified into schizocarps or 1-seeded samaras], sessile [or rarely stipitate]; valves winged or wingless, thick [or membranaceous]; replum much narrower than [or rarely subequaling] the width of the fruit; septum present [or absent]; styles present or absent; stigmas entire [or 2-lobed]. Seeds 1 to several or numerous, mucilaginous or not when wet, wingless or narrowly [to broadly] winged; cotyledons accumbent or incumbent. (Including Brachycarpaeeae DC., Cremolobeae Hayek, Iberideae Godron, Isatideae DC., Senebiereae Godron, Subularieae DC., Thlaspideae DC.) TYPE GENUS: *Lepidium* L.

A natural tribe of about 66 genera (23 monotypic) and some 680 species distributed throughout the world, with the major center of diversification in the Irano-Turanian region, where some 26 genera (13 endemic) and 190 species are found. Other important centers are the Mediterranean region, with 15 genera (four endemic) and about 97 species, eastern and central Asia, with 17 genera (ten endemic) and some 87 species, South America, with ten genera (six endemic) and approximately 86 species, and North America, with 14 genera (eight endemic) and nearly 75 species. In Australia and New Zealand there are about 58 species and five endemic genera, while in Africa (excluding the Mediterranean part) only 25 indigenous species and one endemic genus are found. Nearly half of the species of the tribe belong to five genera: *Lepidium* (175), *Thlaspi* L. (75), *Aethionema* R. Br. (60), *Isatis* L. (60), and *Biscutella* L. (40). Only *Lepidium* is represented by indigenous species on all continents except Antarctica. The Lepidieae are represented in the southeastern United States by six genera and 17 species, of which all, except five of *Lepidium,* are naturalized European weeds. Three additional "wool-alien" lepidiums have recently been reported from waste grounds around wool-combing mills in South Carolina, but none has become established anywhere in the Southeast. *Dithyrea* Harvey was listed for Arkansas by Small (1903), but according to Rollins (1979), the genus does not occur in our area.

Although the Lepidieae are easily distinguished by the angustiseptate siliques (flattened perpendicular to the septum), which are generally less than three times longer than broad (FIGURE 1), the tribal boundaries are sometimes artificially drawn. In some genera the fruits are inflated or only weakly angustiseptate, while in others they are about 20 times longer than broad. Angustiseptate siliques have evolved independently several times within the Cruciferae, and examples outside the Lepidieae are found in *Psychine* Desf. (monotypic; northwestern Africa) and *Schouwia* DC. (two species; North Africa and Arabia), of the Brassiceae; *Lesquerella* S. Watson, of the Alysseae DC.; *Caulanthus californicus* (S. Watson) Payson, of the Thelypodieae Prantl; and *Smelowskia* C. A. Meyer, of the Sisymbrieae DC. The distinction between latiseptate (flattened parallel to the septum) and angustiseptate fruits is usually considered to be highly significant in the classification of the Cruciferae. Both types of fruits, however, occur within the North American members of *Lesquerella* and the

Irano-Turanian genus *Graellsia* Boiss. The latter was divided according to the type of fruit into two genera, each placed in a different tribe (Schulz, Poulter). Angustiseptate, latiseptate, and terete fruits of various lengths are found in *Nerisyrenia* Greene (nine species; North America) and in the North American species of *Smelowskia* (Bacon, Drury & Rollins). These genera cannot be assigned adequately to tribes on the basis of fruit characters and should therefore have the same tribal disposition as their nearest generic relatives. Schulz overemphasized the flattening of the siliques in defining the boundaries of the Lepidieae, and this led to some artificiality in his classification. For example, he maintained *Cardaria* Desv. in the Lepidieae and placed its congener *Hymenophysa* C. A. Meyer, which has globose fruits, in the Euclidieae DC. Similarly, he assigned *Sphaerocardamum* Schauer, with globose fruits, to the Sisymbrieae and proposed *Cibotarium* O. E. Schulz (Lepidieae) for species with angustiseptate fruits (see Rollins, 1984). In my opinion, *Cardaria* (including *Hymenophysa*) and *Sphaerocardamum* (including *Cibotarium*) should be retained in the Lepidieae.

The limits of the Lepidieae are expanded here to include the South American tribe Cremolobeae, which consists of *Cremolobus* DC. (seven species) and *Menonvillea* R. Br. ex DC. (29 species). The latter tribe is recognized by several authors (see Hedge, 1976) and is distinguished by the presence of a gynophore, the absence of a septum, the complete or partial union of the replum margins into a solid or fenestrate stalklike structure, the modification of the valves into one-seeded mericarps, and the frequent attachment of each mericarp to a filiform carpophore derived from the lateral ridges of the style. To those unfamiliar with the Cruciferae, such unusual schizocarpic fruits may justify the recognition of the Cremolobeae as a distinct tribe. Careful study of the entire tribe Lepidieae, however, reveals that several Old World genera, particularly *Biscutella* and *Megacarpaea* DC., have fruits similar to those of the Cremolobeae. I fully concur with De Candolle (1821, 1824) in maintaining the four above genera in the same tribe. Avetisian has recently merged the Cremolobeae with the Thelypodieae and the Lepidieae with the Sisymbrieae. In my opinion, the Lepidieae are a natural tribe that should include both *Cremolobus* and *Menonvillea*.

There is little agreement among various classifications as to the limits of the Lepidieae and the number and limits of its subtribes. The genera that I place in the Lepidieae were assigned to five tribes by Von Hayek and to seven by De Candolle (1821, 1824) and Bentham & Hooker. Four of the 12 subtribes recognized by Schulz are unigeneric and can be easily accommodated in some of the larger ones without drastically altering their limits. At least five of the remaining subtribes, Lepidiinae Prantl, Isatidinae Hayek (probably including *Horwoodia* Turrill), Cremolobinae Prantl (including most of the Iberidinae Hayek), Capsellinae Hayek, and Thlaspidinae Hayek, are sufficiently distinct and may merit recognition. Subtribe Physariinae Prantl and the genera *Lesquerella* and *Physaria* will be discussed in the treatment of tribe Alysseae DC. for the Generic Flora.

Autogamy is fairly common in the weedy members of the Lepidieae. In *Lepidium* and *Coronopus* Zinn it is often associated with either the modification

FIGURE 1. Selected representatives of tribe Lepidieae. a–f, *Capsella Bursa-pastoris:* a, plant with flowers and fruits, × ½; b, flower, × 12; c, flower with sepal and 2 petals removed to show tetradynamous stamens, × 12; d, fruit, × 3; e, replum and septum,

of petals into bristles or their absence, the lack of scent and color, and the presence of only two stamens. Submersed plants of the circumpolar *Subularia aquatica* L. always produce cleistogamous flowers. Monoecism, dioecism, and polyandry, which are very rare in the Cruciferae, are known in only a few species of this tribe. Monoecism has been reported thus far only in *Megacarpaea megalocarpa* (Fischer ex DC.) Schischkin ex Fedtsch., of southeastern Russia and central Asia, while dioecism is known only in three New Zealandic species of *Lepidium,* which are reduced by some authors to subspecies of *L. sisymbrioides* Hooker f. Polyandry has been reported only in the Himalayan *Megacarpaea polyandra* Bentham, which has eight to 24 stamens. Flower color is variable in the tribe, but in *Brachycarpaea juncea* (Berg.) Marais, an endemic of the Cape Province of South Africa, it is described as white, pink, blue, violet, purple, and mauve.

Chromosome numbers are known for at least 260 species (ca. 40 percent of the tribe) and 35 genera. More than 35 percent of the taxa have a base chromosome number of seven, while about 25 percent are based on eight and approximately 15 percent on nine (author's compilation). The lowest chromosome number ($2n = 12$) is found in several species of *Cochlearia* L., while the highest ($2n = 128$) is found in *Cardaria Draba* (L.) Desv. subsp. *chalepensis* (L.) O. E. Schulz. About 67 percent of the species are diploid, and only 23 percent are exclusively polyploid. Polyploidy and aneuploidy probably played important roles in the evolution of *Aethionema, Biscutella, Cochlearia,* and *Nerisyrenia.*

The tribe has been poorly surveyed for chemical constituents. The seeds of only 22 species in nine genera have been analyzed for fatty-acid composition (Kumar & Tsunoda). The scant data show high concentrations of linolenic and eicosenoic acids and lower amounts or the absence of erucic acid in all but six species of *Thlaspi* and *Isatis.* About 40 species and 15 genera have been surveyed for glucosinolates (author's compilation and unpublished data). The dominant compounds appear to be benzylglucosinolate, its ring-oxidized methoxylated or hydroxylated relatives, and several methionine-derived glucosinolates. Only one genus, *Nerisyrenia,* has been thoroughly studied for flavonoids, which have been shown to be very helpful in suggesting species relationships and phyletic groupings, as well as in distinguishing between species (Bacon).

The tribe is almost exclusively herbaceous; only a few unrelated species are typical shrubs. In *Lepidium scandens* Hewson (Australia) and *Cremolobus peruvianus* (Lam.) DC. (Peru) the stems are reported to reach two and five meters, respectively. Both species are said to be vines, a habit unusual in the Cruciferae (Hewson, Khanna & Rollins).

× 3; f, seed, × 25. g, h, *Coronopus didymus:* g, portion of plant with fruits, × 2; h, fruit, × 6. i–l, *Lepidium virginicum:* i, portion of plant with fruits, × 1; j, fruit, × 6; k, seed, × 6; l, embryo (note accumbent cotyledons), × 6. m–o, *L. campestre:* m, fruit, × 6; n, fruit after fall of valve (note apical attachment of seed), × 6; o, embryo (note incumbent cotyledons), × 6. p–r, *Teesdalia nudicaulis:* p, fruit, × 6; q, fruit after removal of valve, × 6; r, seed, × 12. s–u, *Thlaspi arvense:* s, fruit, × 2; t, fruit after fall of valve and 3 seeds, × 2; u, seed (note striate testa), × 6.

Members of the Lepidieae with dehiscent fruits often have mucilaginous seeds, which upon wetting may be dispersed for long distances by adhering to animals. Dustlike or broadly winged seeds, which are uncommon in the tribe, may be dispersed by wind. The majority of indehiscent fruits contain one or two nonmucilaginous seeds, and in many species they are modified into samaras or schizocarpic samaras. Some become strongly inflated and are therefore adapted to dispersal by wind. Samaroid fruits must have evolved independently within the tribe, as evidenced by their occurrence in several unrelated genera. For example, the fruits of some species of *Isatis,* which may be easily confused with the samaras of *Fraxinus* L. (Oleaceae), are quite different from the remarkable fruits of *Pugionium* Gaertner (five species; Mongolia) that have various numbers of wings and appendages. Schulz placed both genera in the same subtribe, but they are clearly unrelated. These genera are also unrelated to either *Brossardia* Boiss. (monotypic; Iraq and Iran) or *Menonvillea,* which have one-winged papery samaras and two- to ten-winged schizocarpic samaras, respectively.

In some of the annual species of *Aethionema,* heterocarpic fruits (dehiscent with several mucilaginous seeds in each of the two locules and indehiscent with a nonmucilaginous seed in the single locule) are produced on the same infructescence. Heterocarpy is genetically fixed in *Aethionema* and is changed little or not at all by environmental conditions (Puech). Voytenko listed heterocarpy in 41 genera of the Cruciferae (including many members of the Brassiceae with segmented fruits), but it appears that only *Aethionema* typically exhibits this feature. In the heterocarpic species the indehiscent fruits differ from the dehiscent ones by the total disappearance of the septum during the early stages of development, the abortion of all but one of the four to many ovules, and the total lignification of the dehiscence line near the replum (Zohary & Fahn). The production of heterocarpic fruits may be an adaptation to different modes of dispersal in steppes and deserts, where most annual species of *Aethionema* occur.

The majority of the Lepidieae occupy mesic habitats, and only a few genera are typically hydrophytic (*Subularia* L.) or xerophytic (*Horwoodia*). In *S. aquatica,* which is usually completely submersed in shallow littoral lakes, the roots and leaves have a remarkably similar anatomy with extensive aerenchyma (Hiltner). The stomata are permanently open, and the guard cells are raised above the leaf surface. The species also grows occasionally as a stunted plant of wet ground, just as its Afro-alpine relative *S. monticola* Schweinf. (Woodhead) does.

Seed size in the tribe shows a very wide range of variation, and the largest and smallest seeds in the Cruciferae are found in *Megacarpaea* and *Mancoa* Weddell, respectively. In *Megacarpaea gigantea* Regel, an endemic of grassy mountain slopes in central Asia, the seeds are about 1.8 × 1.5 cm and may weigh more than 90 mg. Each seed is borne inside a large (4 × 3 cm), broadly winged mericarp. The dustlike seeds of *Mancoa mexicana* Gilg & Muschler, an endemic of the high plains in Jalisco and San Luis Potosí, Mexico, are about 0.3 mm long and weigh only about 0.02 mg (less than one forty-five-hundredth the seed weight of the former species).

The representatives of the Lepidieae in the southeastern United States either are cosmopolitan weeds or are potentially weedy. Some are serious competitors capable of reducing the yield of wheat, while others taint the dairy products obtained from cattle feeding on them. A few species are hosts for several fungi and viruses that attack various cruciferous crops. The young parts of some species are eaten as a salad, and *Lepidium sativum* L. is cultivated throughout the world for that purpose. Many species of *Iberis* L. (candytuft), *Aethionema* (stone cress), and *Thlaspi* (penny cress) are ornamentals grown in rock gardens or flower beds, and a few are used in ornamental dry arrangements. *Isatis tinctoria* L. was formerly grown for woad, a historically important blue dye obtained from its ground, fermented leaves.

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KEY TO THE GENERA OF LEPIDIEAE IN THE SOUTHEASTERN UNITED STATES[4]

A. Seeds 1 in each locule.
  B. Fruits coarsely reticulate or verrucose, often didymous; seeds not mucilaginous when wet; upper cauline leaves 1- or 2-pinnatisect; at least some inflorescences axillary. ..... 15. *Coronopus.*
  B. Fruits smooth, not didymous; seeds mucilaginous when wet; upper cauline leaves entire, toothed, or rarely pinnatisect; inflorescences terminal.
    C. Fruits dehiscent, narrowly winged, retuse to emarginate at apex. ..... 14. *Lepidium.*
    C. Fruits indehiscent, wingless, acute or obtuse at apex. ..... 16. *Cardaria.*
A. Seeds 2 or more in each locule.
  D. Fruits obcordate-triangular; plants with simple, furcate, and stellate trichomes. ..... 19. *Capsella.*
  D. Fruits orbicular-obcordate; plants glabrous.
    E. Flowers zygomorphic; median filaments with broad, scalelike, basal appendage; seeds 2 per locule; basal leaves pinnatifid. ..... 18. *Teesdalia.*
    E. Flowers actinomorphic; median filaments not appendaged; seeds 3 or more (rarely 2) per locule; basal leaves entire or dentate. ..... 17. *Thlaspi.*

14. **Lepidium** Linnaeus, Sp. Pl. **2**: 643. 1753; Gen. Pl. ed. 5. 291. 1754.

Annual, biennial [or perennial] herbs [rarely subshrubs or shrubs to 2 m high], glabrous, papillose, or with simple unicellular trichomes. Stems erect or ascending, sometimes procumbent [very rarely twining]. Basal leaves petiolate, entire to pinnately lobed or 1- to 3-pinnatisect, usually not forming a rosette. Cauline leaves short petiolate or sessile, sometimes auriculate or amplexicaul. Inflorescence an ebracteate, corymbose raceme, greatly [or slightly] elongated in fruit; flowers many, small, pedicellate, perfect [or very rarely imperfect and plants dioecious]. Sepals erect to spreading, not saccate at base, oblong or ovate [rarely orbicular], glabrous or pubescent, sometimes scarious at margin, caducous or persistent until [or after] fruit maturity. Petals oblanceolate, spatulate, obovate, linear, or filiform, sometimes reduced to bristles or absent, longer or shorter than the sepals, usually white, occasionally yellow, pink, or lavender; claws (when present) filiform [very rarely pseudotubular and with a cucullate nectar-accumulating base]. Nectar glands 4 or 6, ovate, triangular, or filiform, median pairs always present, lateral pair sometimes absent. Stamens

[4]The genera are numbered as in the treatment of the tribes of the Cruciferae in the southeastern United States (Jour. Arnold Arb. **65**: 343–373. 1984). Genera 1 and 2 (Thelypodieae) appeared in *ibid.* **66**: 95–111. 1985, and genera 3–13 (Brassiceae) in *ibid.* 279–351.

usually 2, less commonly 6 and slightly tetradynamous, occasionally 4; filaments linear or subulate, wingless, not appendaged, sometimes dilated at base; anthers oblong or ovoid. Ovary 2-ovulate; styles present or absent; stigmas capitate, entire [or slightly 2-lobed]. Fruiting pedicels terete or slightly [to strongly] flattened [or winged], divaricate to ascending [or erect]. Fruits dehiscent, as long as to twice as long as broad, strongly flattened at right angles to the septum, elliptic, oblong, ovate, orbicular, obovate, or obcordate, beakless, sessile [or very rarely borne on a short gynophore], retuse to emarginate [or acute to obtuse] at apex; valves navicular, usually strongly keeled, wingless or extended into a narrow or broad distal wing, 1-nerved, with inconspicuous [or prominent] anastomosing lateral nerves, glabrous or pubescent; replum usually thickened and broader at base; septum narrow, membranaceous, nerveless, elliptic to lanceolate or rhomboid; styles short or long [sometimes obsolete or lacking], included or exserted from the apical sinus of fruit, free or adnate to the apical wing of valve. Seeds 1 per locule, pendulous, narrowly winged or wingless, oblong or oval, rounded or flattened, usually copiously mucilaginous when wet, brown to red or yellow, minutely reticulate; cotyledons entire or very rarely 3-lobed, incumbent or sometimes oblique, very rarely accumbent [or transversely folded (diplecolobous)]. Base chromosome numbers 7, 8, 10, 12. (Including *Cardamon* (DC.) Fourr., *Kandis* Adanson, *Lepia* Desv., *Monoploca* Bunge, *Papuzilla* Ridley, *Sprengeria* Greene.) LECTOTYPE SPECIES: *L. latifolium* L.; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **2:** 164. 1913. (Name derived from Greek, *lepis,* a scale, or more likely *lepidion,* a little scale, in reference to the appearance of the fruit.)—PEPPERGRASS, PEPPERWORT, CRESS, PEPPERCRESS, TONGUEGRASS.

A cosmopolitan genus of about 175 species distributed primarily in temperate and subtropical regions and poorly represented in the tropics and alpine areas, with some 25 species indigenous in North and Central America, 37 in South America, 47 in Australia, New Guinea, and New Zealand, 22 in Africa, and the remainder in Europe, Asia, and the Hawaiian Islands. The genus is represented in the southeastern United States by 12 species, of which five are indigenous, four are introduced from Europe, and three are "wool-alien" weeds recently reported from waste grounds around wool-combing mills in South Carolina.

Four of the seven well-defined sections recognized by Hewson (1982a) are represented in our area. Section LEPIDIUM (sect. *Lepidiastrum* DC.) (petals present; stamens 6; fruits wingless, without apical sinus; styles exserted) is represented in the Southeast by a single species. *Lepidium perfoliatum* L., shield cress, clasping-leaved peppergrass, $2n = 16$, a native of southwestern Asia and probably eastern and central Europe, is a weed of roadsides, waste places, fields, and pastures in North Carolina, Georgia, Tennessee, Mississippi, Arkansas, and probably the other states of the Southeast and is widely distributed elsewhere in North America. It can easily be distinguished by its bi- or tripinnatisect basal leaves, deeply cordate-amplexicaul cauline leaves, and yellow flowers. Two perennials of sect. LEPIDIUM have been brought into North America, but neither has reached our area. *Lepidium latifolium* L., $2n = 24$, is a

successful weed in parts of North America, while *L. graminifolium* L., $2n = 24$, has failed to persist after its initial appearance as a ballast plant.

The monotypic sect. CARDAMON DC. (petals present; stamens 6; fruits narrowly winged, emarginate; styles included in the apical sinus, adnate to the wings; cotyledons 3-lobed) includes only *Lepidium sativum* L., garden cress, $2n = 16, 24$, which is a native of southwestern Asia and northeastern Africa. The species was reported as an escape from cultivation in Tennessee (Gattinger, Hebel), but there is no evidence that it is presently naturalized either in that state or elsewhere in the Southeast.

Of the two species of sect. LEPIA (Desv.) DC. (petals present; stamens 6; fruits broadly winged, emarginate; styles exserted from the apical notch, adnate to the wings; cotyledons undivided) naturalized in North America, *Lepidium heterophyllum* (DC.) Bentham, $2n = 16$, is sporadic in widely separated areas in British Columbia, California, Colorado, and Massachusetts. The second species, *L. campestre* (L.) R. Br. (*Thlaspi campestre* L.), cow cress, field cress, field peppergrass, poor man's pepper, $2n = 16$, is a native of Europe and Asia Minor that grows in fields, waste places, roadsides, pastures, and gardens throughout our area. It is easily distinguished by its sagittate cauline leaves, exserted styles, and large (5–6 × 3.5–4 mm), broadly winged, inflated fruits covered with small vesicles.

The remaining lepidiums in the Southeast belong to sect. DILEPTIUM (Raf.) DC. (petals usually rudimentary or absent; median stamens 2 or 4; fruits narrowly winged or wingless, slightly notched; styles short or obsolete, always included in the sinus), the largest and most diversified section in the genus. *Lepidium virginicum* L., peppergrass, poor man's peppergrass, $2n = 32$, the most widely distributed North American species, probably occurs in every county in the Southeastern States. Of the eight varieties recognized by Hitchcock (1936, 1940, 1945b), *L. virginicum* var. *virginicum* is naturalized on all continents but Antarctica and is the only member of the genus with accumbent cotyledons. Another variety, not previously recorded from the southeastern United States, is *L. virginicum* var. *medium* (Greene) C. L. Hitchc. (*L. medium* Greene, *L. idahoense* Heller, *L. glaucum* Greene), $2n = 32$. It is easily distinguished from var. *virginicum* by its incumbent or oblique cotyledons and its glabrous infructescences. Varietas *medium* is widespread in Texas, Oklahoma, Arizona, and most of the Pacific and Mountain states but is of very restricted distribution and probably introduced in the Southeast (a few collections in Louisiana (*Barkley 37418*, GH; *Lowe 34*, GH), Arkansas (*Demaree 47912*, GH), and Florida (*Brumbach 9171*, GH, and *Wible 801*, A)). The record of *L. Menziesii* DC. from Arkansas (Branner & Coville) probably represents a misidentification of plants of *L. virginicum* var. *virginicum*. Hitchcock (1940) reduced *L. Menziesii* to a variety of *L. virginicum* that is highly localized in Washington.

Another North American species of sect. DILEPTIUM is *Lepidium densiflorum* Schrader (*L. neglectum* Thell., *L. apetalum* of North American authors, not Willd.), peppergrass, green-flowered peppergrass, $2n = 32$, which is also naturalized in Europe and parts of Asia. It occurs in all of the Southeastern States but is less abundant than *L. virginicum*. The two species have often been confused, and some authors (e.g., Smith) have reduced *L. densiflorum* to a

synonym of *L. virginicum,* while Radford and colleagues have omitted it (despite its wide distribution). Plants of *L. virginicum* usually have conspicuous petals equal to or longer than the sepals, accumbent cotyledons, orbicular or elliptic fruits widest at the middle, and pubescent (rarely glabrous) inflorescence rachises with curved, usually subappressed, pointed trichomes. The cotyledons in most varieties of *L. virginicum* are oblique, but incumbent ones can be found in vars. *medium* and *Robinsonii* (Thell.) C. L. Hitchc. In addition, plants of this species tend to produce slightly reduced petals toward the end of the season. On the other hand, plants of *L. densiflorum* always have incumbent cotyledons, reduced or rudimentary petals much shorter than the sepals (or absent), obovate or obcordate fruits widest above the middle, and rachises with short, straight, obtuse papillae. Fruit size is unreliable for distinguishing the two species, particularly if the infraspecific taxa of both are considered. The confusion between *L. virginicum* and *L. densiflorum* may be attributed to interspecific hybridization, as has been suggested by several authors, without supportive experimental evidence. Early North American taxonomists confused *L. densiflorum* with the central Asiatic *L. apetalum* Willd., and a few even suggested that our plant is introduced from the Old World. However, *L. apetalum* is very distinct because of its clavate trichomes and elliptic fruits with small, acute wings. *Lepidium densiflorum* exhibits greatest diversity in the United States, where it is represented by several indigenous varieties that support its North American origin.

The third North American native is *Lepidium oblongum* Small (*L. reticulatum* Thell., *L. Greenei* Thell.), $2n = 16$, which is found in Arkansas (Lonoke, Clay, Miller, and Hampstead counties), Louisiana (Bossier Parish; *Thomas 48608* at NLU), Kansas, Oklahoma, Texas, New Mexico, Arizona, California, Mexico, and Guatemala. It is distinguished from the other lepidiums in our area by its pinnatifid to deeply laciniate cauline leaves, prostrate or ascending stems usually branching near the base, and glabrous fruits with acute wings and V-shaped sinus. Hitchcock (1936) suggested that *L. oblongum* is a South American plant but later (1945b) accepted it as North American. The species has recently been reported as a "wool alien" from South Carolina (Al-Shehbaz, 1986).

Lepidium austrinum Small (*L. austrinum* var. *orbiculare* Thell., *L. austrinum* var. *conspicuiflorum* Thell., *L. lasiocarpum* Nutt. var. *orbiculare* (Thell.) C. L. Hitchc.), $2n = 32$, is another North American member of sect. DILEPTIUM. It is common in Texas, New Mexico, and northern and central Mexico but is rare in Kansas and Oklahoma. Although *L. austrinum* has recently been reported as a "wool alien" from South Carolina, it is probably indigenous to Louisiana. The record (here reported) is based on *Thieret 30012* (GH) from East Carroll Parish, and *Thomas 28857* (NLU) from Grant Parish, Louisiana. The species is distinguished by its hispid stems; dentate or entire cauline leaves; elliptic to ovate siliques with sparse, short, appressed trichomes; and terete or slightly flattened fruiting pedicels with glabrous lower surfaces.

Lepidium lasiocarpum Nutt., which was reported for Louisiana (Thomas & Allen; MacRoberts) and South Carolina (Al-Shehbaz, 1986), is easily confused with *L. austrinum.* Fruits of *L. lasiocarpum* have spreading trichomes, and the fruiting pedicels are either not flattened and with pubescent lower surfaces or

very strongly flattened and with glabrous lower surfaces. I have seen two specimens from Louisiana. One, *Thomas 48606* (NLU), collected from Bossier Parish, belongs to *L. lasiocarpum* var. *Wrightii* (Gray) C. L. Hitchc. The other, *Thomas 34419* (NLU), collected from Ouachita Parish, is intermediate between *L. lasiocarpum* and *L. austrinum.*

The Eurasian *Lepidium ruderale* L. (*L. texanum* Buckley), stinking peppergrass, roadside peppergrass, $2n = 16$, is sporadically distributed in Florida, Alabama, Louisiana, Tennessee, and North Carolina and elsewhere in North America but is more restricted in portions of South America. It is easily distinguished from the other members of sect. DILEPTIUM by its fetid odor, bipinnatifid basal leaves, small (2–2.5 × 1.5–2 mm), ovate to broadly elliptic or oblong fruits with acute apical teeth, and slender pedicels longer than the fruits.

Two other alien representatives of sect. DILEPTIUM have appeared in some of the Pacific States but not elsewhere in the United States. The South American *Lepidium strictum* (S. Watson) Rattan is distributed in California and Oregon, while *L. pinnatifidum* Ledeb., a native of southeastern Russia, is known from a few localities in California. Three other "wool-alien" lepidiums, *L. bonariense* L. (South America), *L. Schinzii* Thell. (Africa), and *L. africanum* (Burman f.) DC. (Africa), have been reported from waste grounds around wool-combing mills in South Carolina (Al-Shehbaz, 1986). They are also "wool-alien" or naturalized weeds in Africa, Australia, and Europe.

Lepidium is a well-defined genus characterized by the angustiseptate, dehiscent, usually notched fruits; the pendulous, usually copiously mucilaginous single seed in each locule; the two or four (sometimes six) stamens; the strongly keeled valves; and the toothlike nectar glands. Its closest relatives are probably *Cardaria* and *Coronopus,* which have indehiscent fruits and usually unkeeled, wingless valves.

Many species of *Lepidium* have been recognized on the basis of minor differences in leaf margin, pubescence, and fruit shape. Species boundaries are sometimes poorly defined, particularly in the polymorphic *L. lasiocarpum, L. virginicum,* and *L. densiflorum,* and a few authors have attributed this variation to hybridization. However, natural hybridization has not been documented experimentally, and its occurrence was suggested by Hitchcock (1936, 1945b) and Howell only on the basis of comparative morphology.

Dioecism in the Cruciferae is known only in *Lepidium sisymbrioides, L. Kawarau* Petrie, and *L. Matau* Petrie (Allan), all from New Zealand. Thellung (1906b) reduced the last two to subspecies of the first, but whether one or more species are involved, nothing is known about the reproductive biology in this complex.

The flowers of *Lepidium* have several adaptations that enforce or promote autogamy, which is very widespread in the genus. In the majority of species the flowers are reduced in size and scentless. In at least 23 percent of the species (author's compilation) the petals are lacking, and in many others they are either rudimentary or inconspicuous. The reduction in flower size is often accompanied by a decrease in stamen number. Of 156 species surveyed by the author, 83 have flowers with two stamens, 20 have flowers with four, and the remainder have flowers with six. Selfing in many species is brought about by anther

dehiscence in the bud long before anthesis. The flowers in *L. campestre* and *L. sativum* are said to be slightly protogynous (Knuth), and those of the latter may be strongly odoriferous, thus promoting outcrossing to a certain degree.

Chromosome numbers have been reported for about 40 species, of which all except five have $x = 8$ and nearly half are either tetraploid or octoploid. Diploid and tetraploid populations have been found in *Lepidium ruderale* and *L. virginicum*. In *L. sativum* diploid and tetraploid plants based on eight and twelve are known (Goldblatt). Vaarama speculated that *L. sativum* is a hexaploid based on $x = 4$, but this interpretation is not supported by facts.

Benzylglucosinolate or its ring-oxidized (hydroxylated or methoxylated) derivatives characterize nearly all of the dozen or so species analyzed thus far. The annotations of M. G. Ettlinger on several sheets in the Gray Herbarium indicate that *Lepidium austrinum* contains benzylglucosinolate, while *L. virginicum* var. *medium* has large amounts of *m*-hydroxybenzylglucosinolate and smaller quantities of the first compound and of methoxybenzylglucosinolate. *Lepidium virginicum* var. *Menziesii* (DC.) C. L. Hitchc. appears to be the single known natural source of ethylglucosinolate (Kjaer & Larsen). The fetid odor produced by *L. ruderale* is caused by benzyl thiocyanate, which results from the hydrolysis of benzylglucosinolate by a special enzyme. The seeds of *L. sativum* contain cucurbitacin, a series of tetracyclic triterpenes very rare in the Cruciferae (Curtis & Meade). Nine species have been surveyed for fatty acids; all show a preponderance of linolenic acid and very little or no erucic acid (Kumar & Tsunoda).

The seed-coat anatomy shows some interspecific differences of taxonomic importance (Jonsell). Cells of the palisade layer have radially and tangentially thickened walls, while those of the epidermis contain large columns of mucilage. Anatomical studies for other parts of the plant are generally lacking. The wood anatomy of the Hawaiian *Lepidium serra* H. Mann and the structure of the fleshy roots of the Peruvian *L. Meyenii* Walp. have been studied by Carlquist and León, respectively.

The seeds of about 85 percent of the species of *Lepidium* (author's compilation) exude an abundant mucilage soon after wetting. Mucilage probably plays an important role in seed germination. It is very strongly developed in species of arid areas (Hewson, 1982a) and in all except three of the weedy species. *Lepidium heterophyllum, L. graminifolium,* and *L. bonariense* have very little or possibly no mucilage. Niemi suggested that the mucilage aids in the dispersal of the seeds of *L. ruderale* by gulls.

Lepidium sativum is cultivated as a salad plant for the peppery taste of its seedlings and young shoots. In the highest and coldest cordilleras of central Peru where no other cultivated plants can grow, *L. Meyenii* is cultivated for its fleshy roots that are eaten boiled or roasted and are also used for flavoring rum (León). The seeds of several species are said to be excellent seasoning for salads, soups, and meat dressing (Fernald & Kinsey). Various species were extensively used for treating warts, tumors, asthma, coughs, and liver diseases. Some are said to have aphrodisiac, laxative, rubifacient, antiscorbutic, and diuretic properties (Caius, Hartwell). However, it is doubtful that the medicinal

properties extend beyond being antiscorbutic. *Lepidium* is important for about 20 weedy species of cosmopolitan or localized distribution.

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15. **Coronopus** Zinn, Cat. Pl. Hort. Acad. Gott. 325. 1757, nom. cons.

Annual, biennial [or perennial] herbs, glabrous or with simple trichomes [or sometimes with minute tubercles]. Stems usually several to many, prostrate or ascending, very rarely solitary and erect. Basal leaves petiolate, 1- to 3-pinnatisect or pinnatifid, occasionally forming a rosette. Upper cauline leaves short petiolate or subsessile, divided [or entire to serrate]. Inflorescence an ebracteate, densely flowered, corymbose raceme, usually axillary or leaf opposed, sometimes terminal or arising directly from the center of rosette, slightly to greatly elongated in fruit; flowers minute, short pedicellate. Sepals spreading, equal, not saccate, caducous or persistent, oblong to elliptic or ovate, usually with a membranaceous margin. Petals undifferentiated [or differentiated] into claw and limb, longer or shorter than the sepals, sometimes reduced to bristles or lacking, white [or violet], oblong or linear-oblanceolate to subulate [or obovate]. Nectar glands [2 or] 4 or 6, minute, usually conical or toothlike. Stamens 6, tetradynamous, sometimes 2 (or 4?) and median; filaments not appendaged, usually dilated at base, caducous [or persistent]; anthers oval, introrse. Fruiting pedicels divaricate [or erect], terete [or flattened]. Fruits indehiscent, strongly flattened at right angles to the septum, broader than long, didymous or reniform to cordate [or obcordate], acute or retuse to emarginate at apex, usually cordate at base; valves 1-seeded, usually nutletlike, with or without an orifice in the area of attachment to the replum, reticulate or coarsely reticulate-rugose to verrucose or tuberculate [or smooth], round or rarely keeled, glabrous [or pubescent]; replum narrowly lanceolate or linear, slender [or thickened], equaling or slightly wider than the fruiting pedicel, persistent [or all or the distal half falling off with the valves]; septum reduced [or lacking]; styles obsolete or prominent, included in the apical notch or exserted and forming the persistent

conical tip of fruit; stigmas capitate. Seeds oblong or reniform [subglobose or oval], sometimes slightly compressed, pendulous, solitary in each locule, non-mucilaginous when wet, minutely reticulate, yellow to light brown; cotyledons incumbent, linear, usually curved near the tip. Base chromosome number 8. (Including *Carara* Medicus, *Cotyliscus* Desv., *Lepicochlea* Rojas Acosta, *Nasturtiolum* Medicus, *Senebiera* DC.) TYPE SPECIES: *C. Ruellii* All. (*Cochlearia Coronopus* L.) = *Coronopus squamatus* (Forsskål) Ascherson; see Int. Code Bot. Nomencl. 1983, p. 350. (Name used by Dioscorides and Theophrastus, probably for *Plantago Coronopus* L.; derived from Greek, *korone,* crow, and *pous,* foot, in reference to the shape of basal leaves. A few authors mistranslate *korone* to crown and suggest that the name corresponds to the radial spreading of basal leaves and lower branches into a crown.)—WART CRESS, SWINE CRESS.

A well-defined genus of ten species, of which four are indigenous to South America and six to Africa, with the natural range of one extending into southwestern Asia and southern and central Europe. Two species are cosmopolitan weeds, and both occur in the southeastern United States. A third, *Coronopus integrifolius* (DC.) Sprengel, is indigenous to Africa and is now naturalized in Australia and eastern Asia.

Coronopus is divided into four well-marked sections, the limits of which correspond fairly well to those originally defined by De Candolle (1821) and slightly altered by Muschler and Schulz (1933, 1936). The Old World sect. CORONOPUS (sect. *Carara* (Medicus) DC.) (stamens 6; petals present; fruits indehiscent, reniform, not emarginate at apex; styles conical; valves keeled) includes two species, of which one is the perennial *C. violaceus* (Munby) Kuntze. The other, *Coronopus squamatus* (Forsskål) Ascherson (*Lepidium squamatum* Forsskål, *Cochlearia Coronopus* L., *Carara Coronopus* (L.) Medicus, *Senebiera Coronopus* (L.) Poiret, *Coronopus Coronopus* (L.) Karsten, *C. Ruellii* All., *C. procumbens* Gilib., *C. verrucarius* (Gars.) Muschler & Thell.), creeping wart cress, swine cress, crowfoot, $2n = 32$, is a cosmopolitan weed with a native range in southwestern Asia, southern Europe, and northern Africa. It is sporadically distributed in the United States, but although it has been reported from Alabama, Florida, Louisiana, and Tennessee, I have not seen any specimens from the Southeast. *Coronopus squamatus* can be distinguished from the other weedy crucifers in our area by its indehiscent, reniform, acute, coarsely rugose-reticulate fruits; its pinnatisect leaves; and its prostrate, much-branched stems.

Section NASTURTIOLUM (Medicus) DC. (stamens 2; fruits didymous, emarginate at apex, splitting into nutletlike, inflated, unkeeled, 1-seeded halves; styles short or obsolete, included in the apical sinus of the fruit) has four species, of which *Coronopus integrifolius* and *C. zambiensis* Jonsell are native to southern and central Africa and two other species to South America. *Coronopus didymus* (L.) Sm. (*Lepidium didymum* L., *Carara didyma* (L.) Britton, *Senebiera didyma* (L.) Pers., *S. pinnatifida* DC., *S. incisa* Willd., *Cochlearia humifusa* Michx., *Biscutella apetala* Walter), swine cress, wart cress, land cress, $2n = 32$, is a cosmopolitan weed widely distributed throughout the Southeastern States along roadsides and in fields, pastures, lawns, gardens, nurseries, and waste places.

The native range of *Coronopus didymus* is controversial. Some North American authors follow Robinson, who suggested that it was originally introduced into North America from Europe, while a few (e.g., Muenscher) have claimed that it is a Eurasian plant. Other authors consider *C. didymus* a South American plant, a view I agree with for two reasons. First, the nearest relative of *C. didymus* is a South American endemic recently described as *C. leptocarpus* Boelcke. Second, the greatest morphological diversity of *C. didymus* occurs in South America, where several varieties and forms have been recognized (Muschler). It is not known how and when *C. didymus* first appeared in Europe and North America, but it was established in some parts of these continents during the late eighteenth and early nineteenth centuries, as evidenced by its repeated description as new species in both continents.

The North African sect. COTYLISCUS (Desv.) DC. includes *Coronopus niloticus* (Delile) Sprengel, an endemic of Egypt, and *C. lepidioides* (Cosson) Kuntze, which is restricted to parts of Tunisia, Algeria, and Morocco. Section XERORRHIZA O. E. Schulz contains *C. rhytidocarpus* (Hooker) Macloskie, of Patagonia, and *C. serratus* (Poiret) Desv., of Argentina and Uruguay. The latter has been introduced recently in Mauritius (Troncoso & Bacigalupo).

Coronopus is easily distinguished by its axillary or leaf-opposed inflorescences, its coarsely reticulate or verrucose to rugose, usually didymous fruits (FIGURE 1h) that break up at maturity into 1-seeded, nutletlike halves, and its nonmucilaginous seeds. It is closely related to *Lepidium.* Muschler suggested that *Coronopus* may represent the end product of parallel evolutionary trends in *Lepidium* that led to the formation of indehiscent fruits. This implies a polyphyletic origin of *Coronopus,* a view not supported by facts. Although Muschler reduced *Delpinophytum* Spegaz. (= *Delpinoella* Spegaz.) to a subgenus of *Coronopus,* the two are remotely related. The former has tiny imbricate leaves, long styles, linear anthers, and copiously mucilaginous, beaked seeds.

Species of sect. NASTURTIOLUM exhibit reductions in flower size, amounts of nectar secreted, petal size, and stamen number. The two anthers usually dehisce in the bud, and pollination may take place long before anthesis. These features undoubtedly indicate autogamy, but protandry and ant pollination have been reported in *Coronopus didymus* by Chauhan (1979a). Cross pollination and slight protogyny have been observed in *C. squamatus.* Several authors have stated that the flowers of *C. didymus* contain two or four stamens. However, the flowers in all but one of the 198 specimens I examined had only two median stamens. In one plant most flowers had two stamens and only a few had four. The petals in *C. didymus* are reduced into subulate or filiform structures misinterpreted as staminodes (Chauhan, 1982b) or as filaments of sterile median stamens (Smith). According to these authors, the petals are lacking, but this implies that all six stamens have a median position facing the outer sepals, a feature not yet found in any crucifer.

Plants of *Coronopus didymus* produce on average some 1600 seeds, but the output of large plants may be as high as 18,000 seeds (Salisbury). A few authors have suggested that the seeds (actually fruit halves) may be transported by strong winds or by birds (McDowall *et al.*), but Salisbury maintains that the

fruits of *C. didymus* and *C. squamatus* are probably distributed in mud on the hooves of animals and that ants also can carry the fruits.

The seed coats of *Coronopus didymus* and *C. squamatus* have palisade cells with evenly thickened inner tangential walls, but the latter species has two layers of thick-walled subepidermis that are lacking in the former (Vaughan & Whitehouse). This anatomical difference supports the disposition of the two species in separate sections.

The leaves and young plants of *Coronopus squamatus* and *C. didymus* are eaten as a salad in the Caucasus and Argentina, respectively. The latter species is cultivated in northern Argentina and is used as a disinfecting infusion for wounds or is mixed with maté (Paraguay tea), *Ilex paraguariensis* St.-Hil., for certain medicinal purposes (La Porte).

Cattle feeding on *Coronopus didymus* develop a disagreeable flavor in their milk (and consequently in their butter). The off-flavor, caused by benzyl mercaptan and benzyl methyl sulfide (Walker & Gray, Park *et al.*), is intensified by heat treatment and cannot be eliminated by conventional techniques (McDowall *et al.*). These compounds are derived from benzyl thiocyanate, which results from the enzymatic hydrolysis of benzylglucosinolate. It has been estimated that up to 20 percent of the butter produced in Australia is weed tainted.

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16. **Cardaria** Desvaux, Jour. Bot. Appl. **3:** 163. 1815.

Perennial herbs, sparsely to densely pubescent with simple trichomes, rarely glabrous. Stems several, erect or rarely decumbent, arising from subterranean rhizomes. Basal leaves petiolate, usually sinuate or lyrate, sometimes dentate or entire. Cauline leaves sessile, sagittate or cordate to auriculate or amplexicaul at base, dentate to denticulate or rarely entire. Inflorescence an ebracteate, densely flowered, corymbose panicle, often slightly elongated in fruit. Sepals erect or spreading, oblong to ovate, not saccate, glabrous [or pubescent], caducous, membranaceous at margin. Petals white, clawed, obovate to spatulate; claw about as long as the limb, usually dilated at base. Nectar glands continuous, subtending the bases of stamens. Stamens 6, tetradynamous; filaments free, not appendaged; anthers oblong or ovate, introrse. Ovary sessile, 2- or 4-ovulate, glabrous [or pubescent]; style usually almost as long as the ovary; stigma capitate, entire, broader than the style. Fruiting pedicels slender, usually spreading. Fruits indehiscent, ovoid or cordate to reniform [or obovoid or subglobose], compressed at right angles to the septum [or not compressed], slightly [to strongly] inflated, glabrous [or pubescent]; valves prominently [or obscurely] 1-nerved, somewhat keeled [or round], reticulate [or smooth]; septum elliptic [or suborbicular], complete [or fenestrate]. Seeds usually 1 per locule, ovoid or ellipsoid, pendulous, wingless, minutely reticulate, reddish brown, mucilaginous when wet; cotyledons incumbent. Base chromosome number 8. (Including *Cardiolepis* Wallr., *Hymenophysa* C. A. Meyer, *Physolepidion* Schrenk.) TYPE SPECIES: *Lepidium Draba* L. = *C. Draba* (L.) Desv. (Name from Greek, *kardia,* heart, in reference to the cordate fruits of some members of the genus.) —HOARY CRESS, WHITE TOP.

A genus of two species native to the Mediterranean and Irano-Turanian regions and widely distributed as naturalized weeds elsewhere in the world, especially in temperate regions, where they grow in fields, waste places, pastures, disturbed sites, and gardens, as well as along roadsides, railroad tracks, and irrigation ditches. *Cardaria* is widespread in the western United States and western Canada but is sporadic in eastern North America and Mexico. It was first collected in the United States in 1862 and in Canada in 1878 (Mulligan & Frankton).

Although *Cardaria Draba* (L.) Desv. (*Lepidium Draba* L., *Cochlearia Draba* (L.) L.), heart-podded hoary cress, hoary pepperwort, white top, is said to be distributed in all of the Southeastern States except Louisiana (Reed), I have not seen any specimens from the Southeast, and the species has not yet been collected from this area. The genus, however, is included here because it occurs in all of the neighboring states and is likely to be found in northeastern Arkansas (Smith).

Some of the many morphological extremes of *Cardaria Draba* have been recognized as distinct species (Rollins, 1940; Mulligan & Frankton). At least two of these are well defined and deserve specific rank. Two subspecies can be recognized in *C. Draba,* but because they are aggressive, perennial, rapidly spreading weeds of similar habitats, they do not have sharply defined ranges. In general, subsp. *Draba* tends to be Mediterranean, while subsp. *chalepensis*

(L.) O. E. Schulz (*Lepidium chalepense* L., *Physolepidion repens* Schrenk, *C. chalepensis* (L.) Hand.-Mazz., *C. repens* (Schrenk) Jarmolenko, *Hymenophysa macrocarpa* Franchet, *C. macrocarpa* (Franchet) Rollins, *H. fenestrata* Boiss., *C. fenestrata* (Boiss.) Rollins, *L. propinquum* (Fischer & Meyer) N. Busch), lens-podded hoary cress, probably is an Irano-Turanian element (Hedge). Both taxa are treated as species by some North American authors and as subspecies by authors elsewhere. I and many others prefer to recognize them as subspecies because they are interfertile and can only be separated by a few continuous characters of the mature fruits. In subsp. *Draba* the fruits are clearly compressed, somewhat carinate, slightly inflated, and usually cordate at the base, while in subsp. *chalepensis* they are slightly compressed, only weakly or not carinate, more inflated, and usually truncate or obtuse at the base. The perforation of the septum shows continuous variation not associated with other morphological characters. Therefore, *C. fenestrata,* which has an incomplete septum, cannot be maintained as a distinct taxon.

Cardaria pubescens (C. A. Meyer) Jarmolenko (*Hymenophysa pubescens* C. A. Meyer), a native of central Asia, is a common, aggressive, and noxious weed in western Canada and the western United States but is only occasional in some other parts of North America. It is easily distinguished from other members of the genus by its sparsely to densely pubescent, noncarinate, strongly inflated fruits.

Although earlier authors (e.g., De Candolle (1821, 1824), Bentham & Hooker, Thellung) reduced *Cardaria* to a section of *Lepidium,* there are significant differences that support maintaining both genera. The fruits of *Cardaria* are indehiscent, inflated, wingless, only slightly or not carinate, and entire at the apex, while those of *Lepidium* are dehiscent, not inflated, strongly compressed contrary to the septum, always keeled, often winged, and emarginate at the apex. Furthermore, the nectar glands in *Cardaria* are continuous and subtend the bases of all stamens; those of *Lepidium* usually form four or six separate teeth. *Hymenophysa* is not sufficiently distinct from *Cardaria* and differs only by its subglobose fruits with a broad septum. Schulz recognized both genera but placed *Cardaria* in the Lepidieae and *Hymenophysa* in the Euclidieae.

The flowers of *Cardaria Draba* are inconspicuous, sweetly scented, and grouped in dense corymbose panicles that are visited by several kinds of insects, particularly bees of the genus *Halictus* (Halictidae) and beetles of the genera *Meligethes* (Nitidulidae) and *Nacerdes* (Oedemeridae) (Knuth). The flowers are protogynous or not and do not reflect ultraviolet light. Both species of *Cardaria* are self-incompatible (Mulligan & Findlay).

Chromosome numbers based on eight characterize both species of *Cardaria,* but the genus is cytologically more complicated than shown by Mulligan & Frankton. The limited number of chromosome counts indicates that *C. pubescens* is diploid ($2n = 16$), while *C. Draba* subsp. *Draba* is tetraploid ($2n = 32$) or octoploid ($2n = 64$) and subsp. *chalepensis* is hexaploid, octoploid, or decaploid (Al-Shehbaz & Al-Omar, Aryavand, Podlech & Dieterle). Natural hybrids between octoploid plants of subsp. *Draba* and decaploid ones of subsp. *chalepensis* are fully fertile enneaploids ($2n = 72$), but the chromosome num-

bers of their offspring range from 66 to 72 (Mulligan & Frankton). Obviously, the genus needs further studies of cytology and hybridization.

Seeds of *Cardaria Draba* subsp. *Draba* contain large amounts of 4-methylthiobutyl and 4-methylsulfinylbutyl glucosinolates (Daxenbichler *et al.*, Procházka), as well as *p*-hydroxybenzylglucosinolate (Al-Shehbaz, unpublished). The green parts contain other glucosinolates not encountered in the seeds (Hasapis *et al.*, Dornberger *et al.*). The other taxa of the genus have not yet been subjected to chemical analyses.

Some anatomical peculiarities of *Cardaria* include the presence of root-hair-like trichomes on the stem just below ground level, the occurrence of large intercellular spaces in the rhizome, and the resemblance of its compact leaf structure (with extremely small, very numerous stomata estimated at 173,355 per square inch) to that of xerophytic plants (Simonds). In seed-coat anatomy *Cardaria* differs from other members of the Lepidieae in having an epidermis with strongly thickened inner tangential walls, a palisade layer with highly thickened radial and inner tangential walls, and a pigment layer three cells thick (Vaughan & Whitehouse).

Cardaria Draba is very difficult to eradicate and is a serious competitor that reduces the yield of wheat lands. Cattle feeding on the plant produce tainted milk and butter. The plant is eaten as a salad or cooked as a potherb in some parts of the Mediterranean region and central Asia. It is also used as fodder. The seeds have a peppery taste and were formerly used as a substitute for pepper.

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17. **Thlaspi** Linnaeus, Sp. Pl. **2:** 645. 1753; Gen. Pl. ed. 5. 292. 1754.

Annual [or biennial or perennial] herbs, glabrous or very rarely with simple trichomes, often glaucous. Stems one or usually several from the base. Basal leaves petiolate [or sessile], forming a distinct rosette or not, entire or dentate to sinuate [rarely pinnately lobed]. Cauline leaves glabrous, sessile, usually amplexicaul, sagittate or auriculate [or very rarely exauriculate] at base, entire or rarely toothed. Inflorescence an ebracteate, densely flowered, corymbose raceme, greatly [or scarcely] elongated in fruit; infructescence loose [or compact]; fruiting pedicels glabrous, usually divaricate. Sepals oblong to ovate, erect, glabrous, equal, not saccate, membranaceous at margin, green [pink or purple]. Petals oblong or oblanceolate to obovate, obtuse [or emarginate], white [rose, purple, or rarely yellow], short [or long] clawed, equaling to twice as long as the sepals. Nectar glands usually present on each side of the lateral stamens, median glands lacking. Stamens 6, tetradynamous; filaments linear, free, not appendaged; anthers ovoid [or oblong]. Ovary sessile, glabrous. Fruits dehiscent, glabrous, strongly [rarely weakly] flattened at right angles to the septum, obcordate to suborbicular [oblanceolate, obovate, obtriangular, or lanceolate], emarginate [or retuse, truncate, obtuse, or acute] at apex, obtuse to cuneate [or attenuate] at base; valves navicular, keeled, nerveless or obscurely nerved, uniformly broad winged [or winged above the middle, or wingless, or terminating in a horn]; replum ovate to lanceolate, usually asymmetric; styles persistent, short to obsolete [or very long and nearly equaling the rest of the fruit], included in the apical sinus [or exserted]; stigmas capitate, entire [or slightly 2-lobed]. Seeds [1 or] 2–6(–10) per locule, ellipsoid or ovoid, often somewhat compressed, wingless, smooth or with concentric, rugose ribs [or papillose or alveolate to slightly reticulate], yellow to dark brown or black, mucilaginous or not when wet; cotyledons accumbent [or very rarely incumbent]. Base chromosome number 7. (Including *Apterygia* (Ledeb.) Galučko (non Baehni), *Atropatenia* F. K. Meyer, *Callothlaspi* F. K. Meyer, *Carpoceras* Link, *Cruciundula* Raf., *Kotschyella* F. K. Meyer, *Masmenia* F. K. Meyer, *Microthlaspi* F. K.

Meyer, *Neurotropis* (DC.) F. K. Meyer, *Noccaea* Moench, *Noccidium* F. K. Meyer, *Pterotropis* (DC.) Fourr., *Raparia* F. K. Meyer, *Syrenopsis* Jaub. & Spach (non *Syreniopsis* Fuchs), *Thlaspiceras* F. K. Meyer, *Vania* F. K. Meyer.) LECTOTYPE SPECIES: *T. arvense* L.; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **2:** 167. 1913. (Name mentioned by Hippocrates for a plant, the crushed seeds of which were used as mustard; derived from Greek, *thlaō* (or *thlaein*), to crush, and *aspis,* shield, in reference to the fruits, which are flattened as if crushed.)—PENNY CRESS.

A taxonomically difficult genus of about 75 species, distributed primarily in the subarctic and the North Temperate Zone of Eurasia, particularly in southern and central Europe, Turkey, and the Caucasus, with five species in western North America, one (*Thlaspi magellanicum* Pers.) in subantarctic South America, and none in either Africa or Australia. Except for the highly polymorphic and widespread *T. montanum* L. of Eurasia and the United States (all of the Pacific, Mountain, and Southwestern states, except Oklahoma), the remaining indigenous North American species, *T. mexicanum* Standley (in the high mountains of Nuevo León, Mexico), *T. arcticum* A. E. Pors. (along the Arctic coast of Alaska and the Yukon Territory), *T. Aileeniae* Rollins (Custer County, Idaho), and *T. parviflorum* A. Nelson (central Idaho to western Wyoming and Montana), are somewhat narrowly distributed or highly localized endemics. The genus is represented in the southeastern United States by three weedy European species.

The genus has been divided into five or six sections on the basis of fruit shape, seed-coat configuration, and elaboration of the wing of the fruit. Several recent authors (e.g., Clapham, Hedge (1965b), and Markgraf) have followed De Candolle (1821), Schulz, and Busch in assigning the lectotype species of *Thlaspi* to sect. *Nomisma* DC. instead of sect. THLASPI, therefore contradicting Article 22 of the ICBN. Section THLASPI (sect. *Nomisma*) (fruits suborbicular, uniformly broad winged, emarginate; styles very short, included in the apical sinus of the fruit; seeds concentrically ribbed) contains three species, of which one is a cosmopolitan weed that occurs in all of the Southeastern States. *Thlaspi arvense,* penny cress, field penny cress, stinkweed, frenchweed, fanweed, $2n = 14$, grows in our area along roadsides and in fields, cultivated land, waste places, and gardens. It is easily distinguished from other crucifers of the Southeast by the sectional characters outlined above.

Thlaspi sect. PTEROTROPIS DC. (sect. *Neurotropis* DC., sect. *Euthlaspi* Prantl, sect. *Chaunothlaspi* O. E. Schulz) (fruits narrowly to broadly obcordate, uniformly winged all around or winged only above the middle; styles long, exserted or sometimes included in the apical notch of the fruit; seeds smooth to alveolate) is somewhat heterogeneous and encompasses the bulk of the genus, including all of the New World taxa. *Thlaspi perfoliatum* L. (*Microthlaspi perfoliatum* (L.) F. K. Meyer), penny cress, $2n = 14, 28, 42, 70$, is a Eurasian plant sporadically distributed along roadsides and in fields, waste places, flood plains, and limestone cliffs in North Carolina, Tennessee, and Arkansas. It differs from *T. arvense* in its smooth and fewer (2 to 4 per locule) seeds, cordate cauline leaves, and smaller (5–7 mm long) fruits.

Another species of sect. PTEROTROPIS is *Thlaspi alliaceum* L., $2n = 14$, which was reported by Radford and colleagues from Rockingham County, North Carolina. This record, which is based on a single collection (*Ahles & Radford 10757* at NCU!), appears to be the first for North America. The species has recently been collected in Indiana and Kentucky (Rollins, pers. comm.). *Thlaspi alliaceum* is easily distinguished by its annual habit; pubescent lower stems; subappressed, oblong, dentate, sagittate cauline leaves; very narrowly winged, slightly inflated, obovate or obcordate fruits; and four or five alveolate seeds in each locule.

The other sections of *Thlaspi,* APTERYGIUM Ledeb. (ca. ten species), CARPOCERAS DC. (ca. nine spp.), and SYRENOPSIS (Jaub. & Spach) Hedge (two spp.), are exclusively Eurasian and contain no weedy taxa.

Thlaspi is a relatively well-marked genus most closely related to and sometimes confused with *Aethionema.* The latter is distributed from the Mediterranean region eastward into Afghanistan and adjacent central Asia, but its center of greatest diversity is in central and eastern Turkey. In general, *Thlaspi* is distinguished by its linear, unappendaged, free filaments and its two- to six-(rarely one- or to ten-)seeded locules. The filaments in *Aethionema* are dilated, winged, or toothed, and those of the median pair of stamens often fuse. The locule usually contains one or very rarely to four seeds. The annual species of *Aethionema* often produce heterocarpic fruits borne usually in compact infructescences, while the perennials often have broadly winged fruits and usually have pink flowers. These combinations of characters are not found in any of the approximately 30 annual and 45 perennial species of *Thlaspi.*

Meyer (1973) segregated *Thlaspi* into 12 poorly defined segregate genera, the boundaries of which were drawn primarily on the basis of minor anatomical differences in the seed coat (see also Meyer, 1979). Of the 107 species recognized by Meyer from Europe, Africa, and the Middle East, only six (in three sections and two series) were retained in *Thlaspi* sensu stricto. In my opinion *Thlaspi* (as traditionally delimited) is a natural group, and I cannot find adequate grounds for dividing it into smaller segregates.

Self-compatibility and autogamy are common in *Thlaspi.* In *T. arvense* and *T. alpestre* L. the stigmas and anthers are held at the same level, and self-pollination results from contact between the stigma and the introrse anthers brought about by the inward bending of the staminal filaments. In the European *T. rotundifolium* (L.) Gaudin and *T. alpinum* Crantz the anthers, which are held below the level of the stigma, turn outward, and autogamy is therefore reduced or prevented. Several species with long styles are protogynous. Riley observed that the stigmas of *T. alpestre* protrude from the floral bud three days before anthesis. During this period the stigmas are receptive, and protogyny and insect visitation account for about five percent cross-pollination in the species.

The flowers of *Thlaspi arvense* are occasionally visited by species of the bee genera *Apis* (Apidae), *Halictus,* and *Dialictus* (Halictidae), the fly genera *Anthomyia* (Anthomyiidae), *Pollenia* (Muscidae), *Eristalis, Metasyrphus,* and *Helophilus* (Syrphidae), and the butterfly *Pieris rapae* (Pieridae). Holmgren and Rochow observed many species of these insect families and of Chrysomelidae

(leaf beetles), Bombyliidae (bee flies), Andrenidae (mining bees), and Miridae (bugs) visiting *T. montanum* in Washington and Wyoming. Peterson (1977a, 1977b) demonstrated that *T. montanum* is pollinated in the alpine tundra of Colorado by the beetle *Phyllotreta albionica* (Chrysomelidae) and by the ant *Formica neorufibarbis gelida* (Formicidae). The reproductive biology of the majority of species has not been studied. Protogyny and autogamy may be more widespread in the genus than is known.

Chromosome numbers have been reported for about 45 species, of which all except *Thlaspi rivale* J. & K. Presl ($2n = 26$; Franzén & Gustavsson) are uniformly based on $x = 7$. The majority of species are diploid. However, *T. alpinum, T. montanum,* and *T. perfoliatum* have both diploid and polyploid populations, while the European *T. goesingense* Halácsy and the Asiatic *T. cochleariforme* DC. are exclusively polyploid. The last species consists of octoploid ($2n = 56$) and 12-ploid ($2n = 84$) populations (Zhukova & Petrovsky, Zhukova *et al.*). All of the New World taxa are diploid, but *T. montanum* var. *montanum* and var. *idahoense* (Payson) P. Holmgren also have tetraploid populations. No counts have been made of *T. mexicanum.* Most counts for *T. perfoliatum* indicate a hexaploid level ($2n = 42$), and although diploid, tetraploid, and decaploid populations have been found (Favarger *et al.,* Hill, Jaretzky), the cytogeography of the species is still poorly understood.

The extensive intraspecific crosses conducted by Holmgren indicate that cross-fertility ranges between 31 and 85 percent in *Thlaspi alpestre* and between zero and 100 percent in *T. montanum.* Crossability between *T. magellanicum* and *T. parviflorum* was 25 to 100 percent and was somewhat lower between the former and *T. montanum* when *T. montanum* was used as the maternal plant. Although the crossability between these species was sometimes high, the first- and second-generation hybrids were largely sterile. The cross *T. alpestre* × *T. montanum,* however, produced fertile first-generation hybrids.

Natural interspecific hybridization appears to be uncommon in *Thlaspi.* Markgraf listed the hybrid between *T. alpinum* var. *sylvium* (Gaudin) Rouy & Foucaud and *T. rotundifolium* var. *corymbosum* (Gay) Gaudin (as *T.* ×*Gremlianum* Thell.), but there is no supporting experimental evidence. Many infraspecific taxa, some of which probably merit specific rank, have been recognized in *T. alpestre, T. alpinum, T. praecox* Wulfen, and *T. rotundifolium.* The taxonomy of these species complexes is rather difficult, and hybridization may have played an important role in their evolution. The affinity of the Asiatic *T. cochleariforme* and the North American and European *T. montanum* is not clear, and although Holmgren reduced the former to a synonym of the latter, *T. cochleariforme* differs in its higher ploidy levels and its unequal petals.

The chemistry of *Thlaspi* has not been studied adequately, and only a few species have been surveyed for fatty-acid composition and for mustard-oil glucosides. Rodman & Chew found large amounts of allylglucosinolate and smaller ones of benzyl and 3-methylsulfinylpropyl glucosinolates in the leaves of *T. arvense.* In the leaves of *T. montanum* they detected traces of isopropyl and 2-butyl glucosinolates in addition to a major constituent tentatively identified as *p*-rhamnopyranosyloxybenzylglucosinolate. Gmelin & Virtanen dis-

covered in *T. arvense* an enzyme that converts allylglucosinolate into allyl thiocyanate, which is responsible for the unpleasant garlicky odor, but Rodman & Chew did not detect this thiocyanate in their sample.

Seeds of *Thlaspi alpestre, T. arvense,* and *T. perfoliatum* have been analyzed for fatty acids (Miller *et al.*). Although they differ from the other members of the Lepidieae in the higher concentrations of erucic acid and lower amounts of linolenic and eicosenoic acids combined (Kumar & Tsunoda), neither *Thlaspi* nor the rest of the tribe has been satisfactorily sampled, and any generalizations are, at best, tenuous.

Two informal groups can be recognized in *Thlaspi* on the basis of the thickening of the radial cell walls of the seed-coat palisade. Meyer (1973, 1979) retained six species with such thickened cell walls in *Thlaspi* sensu stricto despite their marked differences in fruit morphology and seed-surface configurations. He divided the rest of the genus into 11 segregates (all with a thin-walled palisade layer) that differ in fruit morphology and in certain features of the outer epidermis of the seed coat (e.g., cell size and presence or absence of mucilage and the central column). It seems that seed-coat anatomy offers no more than a minimal support to the sectional classification of *Thlaspi.*

Although Howitt (cited in Best & McIntyre, 1975) indicated that the seeds of *Thlaspi arvense* are chiefly dispersed by wind, it is more likely that they are transported with those of various crops. Viable seeds have been found in the dung of cattle and horses and in the droppings of birds. They may retain 11 percent viability after burial for 30 years (Salisbury). The seeds of *T. parviflorum* may be the lightest in the genus (averaging 0.17 mg) and can be easily distributed by wind or rain wash, while those of *T. arvense* are the heaviest, ranging from 0.81 to 1.78 mg (author's compilation). The seeds of *T. perfoliatum* are mucilaginous when wet and may be transported by adhesion to animals.

Early- and late-flowering strains have been discovered in *Thlaspi arvense.* The seasonality of flowering is controlled by simple Mendelian inheritance, and late flowering is dominant. The expression of this character, however, may be altered by vernalization, photoperiod, temperature, and nitrogen supply (McIntyre & Best, 1978).

Several infraspecific taxa of *Thlaspi alpestre, T. montanum,* and *T. rotundifolium* grow on soils with moderate to high nickel and zinc content. Reeves & Brooks have indicated that at least 12 species of *Thlaspi* show unusual accumulation of nickel (to 1000–30,000 μg/g of dry mass) and that 30 European species accumulate zinc to levels higher than 1000 μg/g of the dry mass. The scant data indicate that zinc probably promotes seed germination. Reeves, MacFarlane, & Brooks have suggested that the hyperaccumulators of nickel in *T. montanum* (three varieties) evolved from var. *montanum* growing on non-mineralized soils.

Females of the butterfly *Pieris napi* deposit eggs on the toxic *Thlaspi arvense* without discriminating between it and some of the native western North American crucifers. The larvae apparently die even from the slightest nibble of this plant (Krivda). Rodman & Chew suggested that the repellency and toxicity of *T. arvense* may be attributed to 3-methylsulfinylpropylglucosinolate (or more

likely its isothiocyanate derivative), but Feeny indicated that larval mortality is caused by benzyl thiocyanate, which was not detected in the samples of Rodman & Chew.

Cattle eating considerable quantities of *Thlaspi arvense* may develop hemorrhagic diarrhea, chronic enteritis, gastric distress, nephritis, colic, abortion, apathy, and paralysis of the heart and lungs (Best & McIntyre, 1975). Milk obtained from cows feeding on this plant often develops an unpleasant flavor. Marked reduction in the yield of wheat has been observed in fields heavily infested by the plants. The seeds of *T. arvense* are employed in China to treat eye diseases and as a tonic (Perry), and in Spain as a stimulant and astringent (Caius). The large ornamental fruits of *T. arvense* are often used in dried plant arrangements, the young leaves are said to be edible, and the seeds are occasionally used as a condiment. *Thlaspi rotundifolium* is cultivated as an ornamental rock-garden plant; it forms compact tufts and produces fragrant rose-lilac flowers.

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18. **Teesdalia** R. Brown in Aiton f. Hortus Kew. ed. 2. **4:** 83. 1812.[5]

Annual, usually scapose herbs, glabrous or with simple trichomes. Stems erect or ascending, usually several from the base. Basal leaves petiolate, always in a well-developed rosette, oblanceolate to spatulate [or lanceolate], lyrate to pinnatifid or rarely entire; lateral lobes obtuse [or acute], usually smaller than the terminal one. Cauline leaves (when present) several, small, sessile, linear

[5]Both *Teesdalia* and *Guepinia* Bast. are based on *Iberis nudicaulis* L. According to Stafleu & Cowan (Regnum Veg. **94:** 26, 137. 1976), *Guepinia* and *Teesdalia* were published in July, 1812, and December, 1812, respectively. It is clear, therefore, that *Teesdalia* was illegitimate when published. As clearly indicated by Greuter, *Guepinia* Bast., which is an earlier homonym of *Guepinia* Fries and of two other names of fungi (Martin), cannot be adopted because Article 13.1d of the International Code of Botanical Nomenclature (1983, p. 12) states that the names of fungi adopted by Fries "are sanctioned, i.e., are treated as if conserved against earlier homonyms and competing synonyms." Therefore, *Guepinia* Bast. should be considered rejected.

or oblong, entire or toothed, widely spaced. Inflorescence an ebracteate corymbose raceme, greatly elongated in fruit. Sepals ovate, equal, not saccate at base, ascending to spreading, membranaceous at margin, glabrous. Petals white, obovate to oblong, not clawed; the outer pair much larger than [or subequaling] the inner pair. Nectar glands 4, minute, 1 on each side of the lateral stamens. Stamens 6 and tetradynamous [or 4, equal, and median]; filaments free, linear, white, each with a broadly oblong to ovate or obovate, scalelike, basal appendage appressed to the ovary; anthers oval. Ovary sessile, glabrous, 4-ovulate. Fruiting pedicels slender, divaricate, glabrous or pubescent. Fruits dehiscent, broadly cordate, strongly compressed at right angles to the septum, concave above, convex below, emarginate, glabrous; valves navicular, strongly keeled, margined or narrowly winged distally, with weakly anastomosing nerves; replum ± straight or slightly concave adaxially, strongly convex abaxially; style very short [or absent], included in the apical notch of the fruit; stigma capitate. Seeds 2 per locule, 1 apical and 1 lateral, brown, obovate, slightly flattened, minutely reticulate, wingless, copiously mucilaginous when wet; cotyledons accumbent. Base chromosome number 9. (Including *Folis* Dulac; *Guepinia* Bast., non Fries nec Hepp.) TYPE SPECIES: *Iberis nudicaulis* L. = *Teesdalia nudicaulis* (L.) R. Br. (Name commemorating Robert Teesdale, ?–Dec. 25, 1804, English botanist and horticulturist.)—SHEPHERD'S CRESS.

A very well-defined genus of two species native to Europe, Cyprus, Turkey, adjacent Russia, and northwestern Africa. Members of the genus grow primarily on sandy soil along roadsides and in fields, lawns, and waste areas. Both species are established in parts of North America, and one occurs in the southeastern United States.

Teesdalia nudicaulis (L.) R. Br. (*Iberis nudicaulis* L., *T. Iberis* DC.), shepherd's cress, $2n = 36$, a native of northern and central Europe and an alien in Australia and northwestern Africa, is a naturalized weed infrequently distributed in states of the eastern seaboard (Massachusetts southward into North Carolina) and in Oregon, Washington, and British Columbia. The second species, *T. coronopifolia* (J. P. Bergeret) Thell. (*Thlaspi coronopifolium* J. P. Bergeret, *Lepidium nudicaule* L., *Teesdalia Lepidium* DC.), $2n = 36$, recently reported from California (Quibell & Strother), is a native of southern Europe, Cyprus, Turkey, and northwestern Africa. The two species are superficially similar, but *T. nudicaulis* has obtusely lobed basal leaves, unequal petals, six stamens, and short styles, while *T. coronopifolia* has acutely lobed basal leaves, subequal petals, four stamens, and no styles.

The genus is closely related to *Thlaspi,* and Von Hayek derived it directly from this, while Schulz placed it between *Ionopsidium* (DC.) Reichenb. and *Pachyphragma* (DC.) Reichenb. in subtribe Thlaspidinae Hayek. *Teesdalia* is easily distinguished from these by its pinnatifid rosette leaves, its leafless or very-few-leaved stems, and its appendaged filaments. Species of *Teesdalia* are tetraploids based on nine. Those of *Thlaspi* are diploids and polyploids uniformly based on seven, while species of *Ionopsidium* are diploids with $n = 11$ or 12 or tetraploids based on eight.

Both species of *Teesdalia* are self-compatible. According to Knuth, the flow-

ers of *T. nudicaulis* are visited by many species of insects, including beetles, flies, and bees, particularly members of the genus *Halictus* (Halictidae-Hymenoptera). The species has some peculiar floral features, such as the unequal petals (which give the inflorescence the appearance of a radiate corymb) and the petaloid basal appendages of the staminal filaments (which aid in the accumulation of nectar drops).

The seed oil of *Teesdalia nudicaulis* contains 56 percent eicosenoic acid. The species is among the crucifers richest in this fatty acid and is second only to *Selenia grandis* R. F. Martin, which has a slightly greater percentage (Appelqvist, Kumar & Tsunoda). The seedlings of *T. nudicaulis* contain 2-phenylethylglucosinolate (Cole), but the seeds of this species and of *T. coronopifolia* have not been analyzed.

The seed coat of *Teesdalia* is composed of a mucilaginous epidermis (with a large hollow column on the inner wall of each cell) above thin-walled palisade and pigment layers and a thick-walled aleurone layer (Vaughan & Whitehouse). Seeds of *T. nudicaulis* have an average weight of 0.20–0.23 mg and exude abundant mucilage when moistened. They are probably dispersed by adhesion to animals.

Except for the weedy tendencies of *Teesdalia nudicaulis,* the genus has no economic importance.

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19. **Capsella** Medicus, Pflanzen-Gatt. 85, 99. 1792, nom. cons.

Annual or biennial herbs with simple, furcate, and stellate trichomes. Stems one to several from the base, glabrous or pubescent above. Basal leaves petiolate, usually forming a distinct rosette, very variable in shape and margin, usually entire to lyrately or pinnately lobed. Cauline leaves sessile, usually amplexicaul, auriculate, or sagittate at base, entire to dentate or sinuate. Inflorescence an ebracteate, corymbose raceme, greatly elongated in fruit; fruiting pedicels slender, ascending to spreading. Sepals erect to ascending, oblong to ovate, glabrous or pubescent, not saccate at base, green and with white to red, usually membranaceous, broad margins. Petals obovate to spatulate, white, pink, or red, very rarely yellowish, clawed, as long as or much longer than the sepals, rarely absent. Nectar glands 4, pyramidal or semicircular, 1 on each side of the lateral stamens. Stamens 6, tetradynamous; filaments free, linear, not appendaged; anthers introrse, ovoid to oblong. Ovary sessile, many ovulate, glabrous or very rarely pubescent. Fruit dehiscent, strongly flattened at right angles to the septum, narrowly to broadly obtriangular-cordate, wingless, cuneate at base, emarginate to truncate at apex; valves glabrous, navicular, thin, keeled, obtuse to acute at apex, prominently veined, with the lateral nerves anastomosing near the midvein and usually parallel near the replum; replum narrowly elliptic to lanceolate; septum complete; style short, included or slightly exserted from the apical sinus of fruit; stigma capitate. Seeds (6–)10–20 per locule, brown, oblong, reticulate, mucilaginous when wet, wingless; cotyledons incumbent. Base chromosome number 8. (Including *Bursa* Boehmer, *Rodschiedia* Gaertner, Meyer, & Scherb., *Solmsiella* Borbás.) TYPE SPECIES: *Thlaspi Bursa-pastoris* L. = *C. Bursa-pastoris* (L.) Medicus, typ. cons.; see Int. Code Bot. Nomencl. 1983, p. 351. (Name a diminutive of Latin *capsa*, a box or a case, in reference to the form of fruit, which resembles the medieval wallet or purse.)—SHEPHERD'S PURSE.

A monotypic genus with several infraspecific taxa native to Europe and naturalized elsewhere as cosmopolitan weeds. *Capsella Bursa-pastoris* (L.) Medicus (*Thlaspi Bursa-pastoris* L., *Bursa Bursa-pastoris* (L.) Britton; see Index Kewensis for more than 250 additional synonyms under *Capsella* and *Bursa*), shepherd's purse, pickpocket, shovel weed, hen pepper (Small), $2n = 16, 32$, was introduced into North America from Europe long before the eighteenth century and is generally considered to be the most widely distributed crucifer and the second most widely distributed weed on earth (Coquillat). It grows along roadsides and in waste places, lawns, gardens, and cultivated grounds throughout the Southeastern States.

There has been some controversy in treatment of *Capsella* as monotypic or, alternatively, as consisting of four or more species. Undoubtedly, the 200 or more "species" recognized by Almquist (1907, 1921, 1923, 1929) and Shull (1929), which are based on very minor differences in the shape of the basal leaves and fruits, are nothing but biotypes of *C. Bursa-pastoris*. The variation in nearly all features is continuous, and it is often difficult to draw meaningful and reliable lines in this complex. The genetic bases for most of the variation in leaf and fruit morphology were shown by Shull to be controlled by simple Mendelian inheritance, the phenotypic expression of which can be altered by the environment.

Chater recognized five species in *Capsella* separated primarily by petal color and by petal and style lengths. However, Svensson has clearly demonstrated that these characters are unreliable and that the difference in chromosome number between *C. Bursa-pastoris* and *C. rubella* Reuter does not correlate with curvature of the lateral margins of fruit, petal/sepal ratio, color of sepals and petals, or habitat and geographic distribution. These alleged differences in morphology do not correlate with each other either, but they have been utilized in many floras (e.g., Chater, Fernald, Hedge, Markgraf) as the bases for separating *C. Bursa-pastoris* from *C. rubella*. In my opinion, Svensson is fully justified in treating *Capsella* as monotypic, in considering *C. rubella* as a variant not deserving specific rank, and in suggesting that *C. grandiflora* (Fauché & Chaub.) Boiss. and *C. thracica* Velen. may merit no higher than subspecific rank. A similar conclusion was reached earlier by Davis & Heywood, who suggested (p. 379) that ". . . the taxonomy of the group remains intractable beyond the recognition of the one species, *C. Bursa-pastoris,* containing a number of infraspecific taxa." *Capsella rubella* and *C. grandiflora,* which represent the two opposite extremes in floral morphology in the genus, produce fully fertile hybrids (Riley, 1932) and are indistinguishable in their fatty-acid composition (Mukherjee *et al.*) and in seed-coat anatomy (Vaughan & Whitehouse). Plants comparable to *C. rubella,* as interpreted in the floras cited above, occur in North and South Carolina, Florida, Alabama, and Louisiana.

Perhaps the nearest relatives of *Capsella* are *Hutchinsia* R. Br., *Hymenolobus* Nutt. ex Torrey & Gray, and *Cochlearia* L. From these it is easily distinguished by its rosulate, nonfleshy basal leaves, its stellate, furcate, and simple trichomes, and its many-seeded, obtriangular-cordate fruits. Several authors have united *Hymenolobus* with *Capsella,* but this is not justified, and the former is more

allied to and perhaps not sufficiently distinct from *Hutchinsia,* which has two- to four- (instead of many-)seeded fruits characteristic of *Hymenolobus.* The direct relationship between *Capsella* and *Neslia* Desv. with *Camelina* Crantz, as proposed by Von Hayek, reflects no more than superficial resemblances.

The remarkable uniformity within a given population of *Capsella Bursa-pastoris* is attributed to extensive inbreeding and particularly to autogamy. Some ecological factors, however, may play an important role in determining the amount of selfing. Hurka, Krauss, Reiner, & Wöhrmann showed that dry and sunny days favor outcrossing and induce the formation of protogynous flowers, while cloudy or rainy days (i.e., low light intensity, high atmospheric humidity, and temperatures above 15°C) lead almost exclusively to selfing. Furthermore, cold weather appears to suppress the formation of normal anthers. Gynomonoecious and gynodioecious plants may be produced early in the season, while functionally perfect flowers are produced in early spring (Knuth), and male-sterile ones may be encountered toward the end of the season (Stace). Numerous species of bees, beetles, butterflies, flies, hoverflies, and thrips have been observed as occasional visitors of the flowers (Knuth).

Self-incompatibility has been reported in forms of *Capsella Bursa-pastoris* known as *C. grandiflora* (Riley, 1932, 1936). Although Riley suggested the presence of three mating groups controlled by two genes (each with two alleles) showing epistasy and dominance, Bateman believed that self-incompatibility in *Capsella* can be better explained as controlled by one locus with at least three alleles showing dominance.

Two chromosomal levels, diploid ($2n = 16$) and tetraploid ($2n = 32$), are known in *Capsella Bursa-pastoris.* Crosses of plants with the same chromosome number always yield fully fertile offspring, regardless of the morphological differences between the parents. On the other hand, crossing diploid and tetraploid plants produces sterile triploids with abortive pollen and shriveled seeds. Such triploid hybrids are widely distributed in nature and have been named *C.* ×*gracilis* Gren. They are said to be derived from *C. Bursa-pastoris* and *C. rubella.* Many authors have considered the last "species" a diploid, but the painstaking work of Svensson indicates that diploid and tetraploid populations in this complex are morphologically indistinguishable, even though the tetraploid tends to have slightly larger sepals, petals, fruits, and seeds. The tetraploid plants flower earlier than the diploid and appear to have wider distribution.

The genetic basis of variation in *Capsella* was studied by Shull (1929), who grew more than half a million individuals and analyzed some 4000 pedigreed lines. He crossed *C. Bursa-pastoris* (obtriangular fruits) with *C. Heegeri* Solms (elliptic fruits) and discovered that the latter is nothing but a double recessive mutant segregating in the second generation at a ratio of approximately 15:1. The mutant was treated earlier as the basis of a new genus, *Solmsiella.*

The embryogeny of *Capsella* has been more thoroughly studied than that of any other crucifer and has been included in numerous textbooks of plant anatomy and embryology as typical of the dicotyledons. The embryogeny is not repeated here, and further details are found in the classic works of Schaffner, Souèges, and Rijven. The ultrastructure, morphogenesis, and growth and de-

velopment of embryos have been thoroughly covered in many papers listed in the references.

Plants of *Capsella* contain high concentrations of allylglucosinolates and small amounts of the alkaloids tyramine and sinapine. The fatty-acid composition of the diploid "*C. rubella*" and "*C. grandiflora*" is indistinguishable from that of the tetraploid *C. Bursa-pastoris*. Seeds from the temperate regions tend to have a higher oil content than those from colder areas (Mukherjee *et al.*). The genus resembles most members of the Lepidieae in having high concentrations (20–35 percent) of linoleic and linolenic acids and negligible amounts (0.2–0.7 percent) of erucic acid.

An anatomical peculiarity of *Capsella Bursa-pastoris* is the derivation of the interfascicular cambium of the shoot from the starch sheath (Hurka & Büchele). The seed coat of this species is indistinguishable from that of "*C. rubella*" and "*C. grandiflora*" and is composed of palisade cells broader than long and with thickened radial and inner tangential walls, and of epidermal cells with a large, solid column protruding into the lumen from the inner tangential wall (Vaughan & Whitehouse).

A single plant of *Capsella Bursa-pastoris* may produce 5000–90,000 (usually 30,000–60,000) small seeds weighing about 0.1 mg (Hurka & Haase). The mucilaginous epidermis of the seed coat aids in long-distance dispersal by adhering to animals and farming machinery. The seeds may retain viability after passing through the digestive tracts of birds and earthworms. The species shows a remarkably high degree of phenotypic plasticity, and the plant may produce fruits within a few weeks after seed germination. Although seed size is genetically controlled, it is also phenotypically plastic; plants of severely cold climate usually produce larger seeds than those in more favorable areas (Hurka & Benneweg).

Seeds of *Capsella* show pronounced dormancy that can be broken experimentally by cold treatment after imbibition. An increase in nitrate level and a fluctuation in temperature can replace the requirement for stratification and are therefore important in breaking seed dormancy in nature. Cold-treated seeds may fail to germinate unless exposed to light at the soil surface (Popay & Roberts, 1970a, 1970b).

Barber (1978a, 1978b) indicated that the seeds of *Capsella Bursa-pastoris* show protease activity in their mucilaginous sheath and are capable of uptake and incorporation of radioactively labelled amino acids. Seeds attract soil nematodes, protozoans, and bacteria, causing some mortality, and they may even derive some nutrients from them. Barber suggested that these adaptations may supplement the nutrition of the germinating seed but questioned whether the seeds are truly "carnivorous."

Many medicinal properties have been attributed to *Capsella Bursa-pastoris*, and various preparations have been prescribed to treat tumors, nasal and internal bleeding, stomach disorders, irregular menstruation, kidney complaints, dysentery, and dropsy. The plant is also considered antiscorbutic, stimulant, astringent, and diuretic (Caius, Hartwell, Perry). The young rosettes are eaten as a salad and are regarded as an excellent substitute for spinach and a rich source of vitamin C. The plant is sold in some parts of China and India.

Cattle feeding on large quantities of it often produce tainted milk. Finally, in addition to being a troublesome weed, *C. Bursa-pastoris* is a host for several fungi and viruses that attack cruciferous crops.

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EVOLUTIONARY CLASSIFICATION IN BOTANY, 1960–1985

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Evolutionary systematics has been the prevailing school in botanical systematics in studies at the genus level and above throughout the century. It attempts to incorporate information about amount of change and genealogical relationships between plants into a classification convenient for the user. Most of the principles currently used for grouping and ranking in evolutionary systematics (see Cronquist, 1957, Thorne, 1958, and Takhtajan, 1969, for references) are simply general guidelines that are difficult to use in particular cases. They originated in comparable principles developed by pre-Darwinian botanical and zoological systematists, although the terminology used then was different. Relationships in pre-Darwinian systems were generally described in terms of webs, nets, maps, or even stellar systems (Planchon, 1860). These are all reticulating structures, sometimes with surface features, but with little or no vertical—let alone temporal—dimension. Taxa were discussed as being "related" directly to a great variety of other taxa and were polythetic in nature—they had no unique or constant characters, but several characters were held in common, each member of the taxon having many of them (see Stevens, 1984b, for references).[2]

In this paper I discuss some principles that control the formation and ranking of groups in evolutionary systematics, emphasizing relationships at and above the level of genus in flowering plants. The discussion will focus on practice since 1960. I shall not discuss systematics at the species level and below since developments there are largely independent (Heywood, 1964; Dean, 1979; Hagen, 1983); the description of species largely from herbarium material does, however, face several of the problems mentioned below. As a final qualifier, although I discuss particular aspects in the practice of evolutionary systematics, these by no means define the "school" in its entirety. The problems are most obvious when we deal with difficult groups of plants, which most of us do some of the time. In such situations we often form taxa by the process of chaining, discussed below; as Barabé (1984) notes, natural families formed by chaining

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[2] Polythetic groups may of course be of interest to a phylogenetic systematist (e.g., see Gauld & Mound, 1982). Groups that are polythetic at the level of the distribution of characters in known taxa may be monothetic at the level of the lineage ancestral to the whole group. In addition, evolutionary systematists also describe other than polythetic groups. Groups may be formed by emphasizing that all members possess a particular character or characters perhaps unique to that group (Burtt, 1964; see Stevens, 1984b, for additional references). However, this way of forming groups is far from universal.

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("familles par enchainement") are common. However, that these practices may seriously affect the significance of our work should make us pause for thought.

This paper elucidates the nature of the problem faced by evolutionary systematics and systematists adumbrated earlier (Stevens, 1984b)—the persistence of preevolutionary taxonomic methodology and style of explanation in evolutionary guise. I shall show that the interpretation of the frequently polythetic early-nineteenth-century higher taxa in an evolutionary context has led to an assertion that parallelisms were widespread. This assertion, in turn, led to the adoption (in point of historical fact, the persistence) of grouping by variants of overall similarity when forming taxa. Various conventions have been adopted to heighten the apparent distinctiveness of such taxa. In addition, there has been widespread use of parallelisms as evidence of relationship; this use was connected to the adoption of taxonomic monophyly. There was no encouragement to search for a genealogy that would imply lineages (and groups) with distinctive and unique characters. Polythetic groups do not have such characters (by definition); fossils were also lacking. In the absence of such a genealogy and characters, intermediate groups featured prominently as ancestors in evolutionary discussion.

The underlying problem is that adoption of evolutionary terminology allowed the complete incorporation of preevolutionary taxonomic practices and taxa into "evolutionary" systematics. In addition, an underlying belief of systematists in the reality of natural groups made evolutionary systems difficult to challenge and discouraged analysis of taxonomic principles. The whole story turns on the interrelationships between polythetic groups, parallelisms, overall similarity, and taxonomic monophyly. Hence, we find that the situation is far more complex even than the "anastomosing plexus of reasoning and evidence" (Johnson, 1968, p. 26) that is phylogenetic taxonomy, and that there is a major element in evolutionary systematics that evolutionary biologists had not bargained for.

Davis (1978) saw a broadly phenetic classification, a fair characterization of much evolutionary systematics, as we shall see, behaving like the phoenix: continually rising from the ashes of its predecessor and always different, yet basically the same. But the issue is not that of some alteration within the constraints of a methodology that has persisted basically unchanged for about 300 years (that is young, for a myth); it is the very relevance of this methodology for addressing the evolutionary questions in which we are interested, yet which such broadly phenetic classifications have been used to address.

DEFINITIONS

There is confusion in the discussion of evolutionary classifications because some of the key words have several definitions. Users of the classifications have often been unaware of these potentially conflicting definitions and have simply translated ambiguous words in their own way; this point will be developed in the Discussion. In addition, the principles of the evolutionary school of systematics must be outlined since these also are potentially conflicting.

The word "evolution" itself is particularly ambiguous as there are two major

components to evolutionary pattern. In the rest of the paper, "cladistic" and "cladistic relationships" will refer specifically to the branching component of evolution, and "patristic" and "patristic similarity" to general relationships due to common ancestry (for the latter, see Davis & Heywood, 1963; Sokal & Camin, 1965). The word "phylogeny" often subsumes both components (e.g., see Turrill, 1942). The term "genetic," as in the frequently expressed hope (for example, of Stebbins & Crampton, 1961) that a classification reflect probable genetic evolutionary relationships, is also ambiguous. It may mean overall similarity, basically patristic relationship, or unique similarity in specific elements, basically cladistic similarity, or phylogeny (as in the use above). There are comparable problems with the word "relationship" as well (Walters, 1964).

Another important but ambiguous word is "monophyly." Taxa in evolutionary classifications must be monophyletic by definition (Sokal & Sneath, 1963). There are, however, three definitions of this term.

1. A group is monophyletic if it arises from another group of the same or lower formal rank (taxonomic monophyly: Turrill, 1942). This was the definition used by Simpson (1945, 1961), who is much cited by Cronquist (1963, 1975, 1985). Alternatively, a taxon may be considered to be monophyletic only if it arises from a taxon of lower rank than itself, but the possibility of multiple, independent origin at this lower level is still allowed. Taxonomic monophyly is probably the commonest kind of monophyly used by evolutionary botanists (Merxmüller, 1977; see Davis & Heywood, 1963, pp. 44–48, for a clear discussion, and Verlaque, 1984, for the principle in action).

2. A definition used by Wernham (1912) and followed by Heslop-Harrison (1958) is that a monophyletic taxon is derived from a single ancestor (species) of that taxon—genealogical monophyly (Gilmour, 1940; Turrill, 1942). Thorne (e.g., 1973) adopted this definition. However, not *all* descendants of the ancestral species need be included in such a monophyletic taxon, and it is often called paraphyletic (e.g., Mayr, 1982, pp. 227, 235; see also the concept of convexity, Estabrook, 1978). This is a common zoological definition of monophyly, but it is less common in botany. Genealogical monophyly is closest to the definition of monophyly as the term was originally used (Haeckel, 1866, explained in more detail later—e.g., Haeckel, 1878, pp. 371 *et seq.*; see Ashlock, 1984). In some cases genealogical and taxonomic monophyly simply reflect differences in the level at which group membership is specified, but this level difference is rarely spelled out in detail (see Heslop-Harrison, 1958; Simpson, 1961; Heywood, 1966).

3. A third definition, which will be referred to as strict monophyly, is that all (but only) the known descendants of an ancestral species must be included in a taxon for it to be monophyletic.

Associated with the term "monophyly" is the term "homologous." Homologies refer to similarities between monophyletic groups, and they include derived characters reflecting unique, genealogical relationships between these groups, characters that arose independently in two or more groups (parallelisms—see below), and widespread and primitive characters that arose once but are found in groups other than those under consideration. For this and other reasons, the exact meaning of the term "homology" has long been a matter of

dispute (Lankester, 1870; Mivart, 1870; Sattler, 1984; Stevens, 1984c; Tomlinson, 1984).

Finally, definition—or even circumscription—of the school of evolutionary systematics is difficult; its proponents cover the entire spectrum from near-pheneticists to near-cladists. The "evolutionary systematics" being discussed here does not include the school of phylogenetic systematics developing from the work of Wagner (1952) and Hennig (1966) in particular, although there are elements of it in Wagner's early ideas (Stevens, 1984b), nor does it include that branch of phenetics that eschews evolutionary interpretations of dendrograms.[3]

The important elements of evolutionary taxonomy as generally practiced at higher levels in botany can be summarized as follows:

1. Goals. Classifications should a) reflect both cladistic and patristic elements of evolution, b) be general purpose, and c) be made up of predictive taxa.

2. Group formation. Groups are formed of members that share several correlated characters. Primitive and derived similarities are often not distinguished, nor—sometimes—are characters that are common and uncommon in the group. Some characters are more heavily weighted than others, but all rules bearing on weighting have exceptions.

3. Classification. a) Rank is proportional to the magnitude of the differences between taxa, but the larger the taxon, the smaller the gap between it and other taxa need be. b) All taxa must be "monophyletic." c) Previous taxonomic history and ease of recognition of groups may also legitimately influence both the rank and the circumscription of taxa.

4. Attitude toward evolutionary relationships. Higher taxa show ancestor-descendant relationships. Characters of lineages are little discussed, except in the case of the angiosperms as a whole. The more characters two taxa have in common, the closer cladistic relationships are considered to be, and the less the time since divergence.

Although not all evolutionary systematists would subscribe to all these elements (and a number hold additional ones, as will be discussed), the elements are common among them. Using the lettering and numbering above, Cronquist (1968) supports 1a–c, 2, 3a–c, and 4; Thorne (1976), 1a, c (implied), 2, 3a (rank strictly proportional to gap), b, and 4; Takhtajan (1980), 1a, 2, 3a (implied), b (especially with higher taxa), and 4; Estes and Tyrl (1982), 1a–c, 2, 3a, b (implied), c, and 4 (little discussed); and Jeffrey (1982), 1a (implied), b, c, 2, 3a (implied), b (implied), c, and 4 (little discussed).

The issue of the relationship between classification and comparative biological thought in general is not emphasized in most of the works being discussed,[4]

[3]Note that in citing authors as having held certain views, I do not imply that those authors necessarily still hold them, or that they held them consistently throughout their work. It is of interest that a more or less pronounced cladistic approach is evident in recent work of a number of authors cited (e.g., Dahlgren, 1983; Dahlgren & Rasmussen, 1983; Takhtajan, 1983).

[4]Pheneticists in particular have been much concerned about apparent problems of circularity with phylogeny and classification (Sokal & Sneath, 1963; Sneath, 1983; Stevens, 1984b; see also Hull, 1967, for a good discussion). Other workers have stressed studies at lower levels (biosystematics) as being the best—or indeed the only—way to study evolution and to avoid this and other problems.

thus the almost contingent nature of much evolutionary thought on the structure of classifications seems to have passed almost unnoticed. However, Schaffner (1911, p. 409) observed that "the views of all botanists, whether they deal directly with classification or not, must be more or less influenced by the scheme of supposed relationships which they follow" (see also Robinson & King, 1985); these "views" are taken from classifications. Mason (1950) realized that there were problems: botanists using taxonomic groups should judge them before use, since reasonable differences of opinion (for example, concerning rank) occur; taxa of the same hierarchical rank belonging to different higher taxa might not be comparable. Thorne (e.g., 1976) is somewhat exceptional in his attempts to introduce equivalence into the gaps that separate taxa of the same rank.

FORMATION OF HIGHER TAXA

Much value is placed on "experience," "instinct," and "intuition" when forming groups and recognizing relationships (e.g., see Cronquist, 1968; Nordenstam, 1978), yet details of the mental processes involved remain unclear. As a result, there is a very real danger that a mythology about how the experienced taxonomist's mind works will develop. Clayton (1983, p. 151) has recently suggested that a "working taxonomist seems . . . to recognise that characters can be ranked according to their observed behaviour in the overall system." Jeffrey (1983, p. 7) is more explicit: "Cladistics then emerges as merely the explicit codification of what has long been the practice of classical or intuitive taxonomy" (see also Guédès, 1982). A claim is then made that the intuitive (i.e., cladistic) method results from the way that the human mind has evolved "to deal with sense data in the way which is of the greatest utility to man himself" (Jeffrey, 1983, p. 7)—it is effectively the result of natural selection. (Riedl [1978, 1982] made comparable claims; see Plotkin [1982] for further references.) However, other authors have seen the situation differently. Heywood (1964, p. 3) considered that phenetic classification "was the sort of activity which taxonomists undertake, or aim to undertake." This viewpoint is often more nearly accurate, and one of the seminal papers of the phenetic school (Cain & Harrison, 1958) attempts to analyze how taxonomists generally make judgments of affinity (see also Stafleu, 1966; Stevens, 1984b). The cases discussed below of both synthetic (overall similarity) and analytic (*methodi cloacae*) group formation clarify some of the ways in which taxonomists "intuitively" make groups.

EVALUATION OF CHARACTERS

Evolutionary systematists use weighted similarity in homologous characters when establishing relationships. Homology is established by using various criteria to assess similarity between structures (see Tomlinson, 1984). This approach may be extended when deciding that two characters belong to the same morphocline—a series or chain of characters is established so that differences between adjacent members of the series are small (e.g., Melville, 1983, including

references; Croizat, 1964; cf. Sattler, 1984, and Stevens, 1980, 1984c). The chaining procedures used to establish homologies are similar to those discussed below used in group formation.

Although characters are weighted, Takhtajan (1980, pp. 231, 232) noted, ". . . weighting can be only *a posteriori,* that is, based on experience. It is determined by the trial and error method, based on the personal experience of a systematist as well as on the experience of his predecessors and colleagues" (see also Barabé & Brouillet, 1982). Weighting is considered to be extremely difficult because of convergence, large morphological effects caused by small genetic changes, and the differing importance of a single character in different parts of the taxonomic system (Davis & Heywood, 1963; Sneath & Sokal, 1973; Dahlgren, 1975; and practically all other authors): ultimately, problems in weighting stem from the nature of groups. The phenomenon of heterobathmy—different kinds and amounts of change in different lineages—also concerns many botanists, especially those from Europe (see APPENDIX 1). There is no reliable rule that can determine the importance of a particular character in evolutionary classifications, since every rule has numerous exceptions (see, for example, Wagenitz, 1963). All these problems make the use of weighting in evolutionary taxonomy quite capricious, and evaluation of the characters considered to support relationships is difficult (e.g., see Meeuse, 1964; Barabé, 1984).

GROUP FORMATION BY WEIGHTED OVERALL SIMILARITY

One common way of forming groups is to look at the co-occurrence of as many characters as possible; some form of overall similarity is used (e.g., see Benson, 1957; Hamann, 1962; Davis & Heywood, 1963; Stafleu, 1965; Burtt, 1966; Cronquist, 1968, 1980; Becker, 1974; Dahlgren, 1975; Takhtajan, 1980; Dressler, 1981; Dahlgren & Clifford, 1982; Barabé, 1984). Different kinds of similarities are often not clearly distinguished when groups are being formed: derived characters, primitive characters, and parallelisms alike are treated as indicators of "evolutionary affinity"; all may be "homologous."

An example is afforded by my placement of *Wittsteinia* F. Mueller in a separate subfamily within the Ericaceae (Stevens, 1971). My rationale was that *Wittsteinia* had several characters in common with other members of the family: an inferior ovary (elsewhere found in two tribes in the family), serrate petals (found in a few unrelated genera in the family; not in taxa with inferior ovaries), uniseriate hairs (a similar situation to serrate petals; the hairs in locations different from those in *Wittsteinia*), and so on. Clearly, variation in such characters within many sympetalous groups is such that *Wittsteinia* could probably have been placed in other families with comparable ease.

My placement clearly flouts the advice of looking for correlated variation, but this is made evident only by detailing the distribution of the characters in the family. At the familial level the characters are correlated—the Ericaceae and *Wittsteinia* have many characters in common. At the generic level they are not—individual genera of the Ericaceae and *Wittsteinia* have few characters in common. Very often placements are made because higher taxa "have"

characters, but the detailed distribution of such characters within those taxa is not discussed. The use of numerous characters in group formation in such cases is hardly appropriate.

I also did not realize that only characters of a certain kind were likely to be helpful in establishing cladistic (or—more generally—"evolutionary") relationships. For example, the occurrence of uniseriate hairs in the Ericaceae (basically in *Epigaea* L. and *Wittsteinia*) should not enter into the discussion. Since other characters show that the groups in which that character occurs are not immediately related, it is not a unique character signifying relationship. Of course, the fact that *Wittsteinia* had been placed in the Ericaceae influenced the final decision about relationships and taxonomy, but the methodology used allowed it to be retained there. It is now known that *Wittsteinia* should properly be compared with *Alseuosmia* A. Cunn., of the Alseuosmiaceae (see Van Steenis, 1984). The two have a number of similarities, at least some of which appear to be restricted to them (and perhaps a couple of other genera) when compared with their possible relatives. These similarities include uniseriate hairs in the same position, serrate petals, and perhaps also nodal and xylem structure (see Stevens, 1971; Gardner, 1978).

A similar example is the inclusion of the Barbeyaceae in the Urticales (e.g., see Cronquist, 1981), which apparently strengthens the case for including the Urticales in the Hamamelidae. The Barbeyaceae have primitive characters of the Hamamelidae that are not found in the Malvales (Dilleniidae), another possible relative. These characters are not even unique to the Hamamelidae, being found also in some other Dilleniidae (and elsewhere).

In the method of forming groups discussed above, generally only the occurrence of characters within the two taxa is considered. Because of the great variability and heterogeneity of some groups, it may be easy to find relationships between groups, especially if the distribution of a character within groups is not considered important (e.g., see Benson, 1957; Clayton, 1983). As multiple, largely pairwise comparisons are carried out over time, taxa may be chained together, again with the results that taxa at opposite ends of the chain may have little in common. The method of independent pairwise comparison of taxa is close to the single linkage clustering method and similar algorithms described by Sneath and Sokal (1973). Interestingly, one of the less-desirable features of this algorithm is its propensity to produce chaining of taxa, with groups adding on singly and sequentially to the first group (Clifford & Stephenson, 1975). Polythetic groups will tend to be the result.

For example, Hamann (1961) commented on the extent of similarity relationships shown by the more heterogeneous monocotyledonous families. Cronquist (1983) found no difficulty in assigning rather problematic groups to the Violales (e.g., the Huaceae) and Rosales (Surianaceae, Rhabdodendraceae, Anisophylleaceae); those orders were already large and heterogeneous, so further groups deemed to be related could be added easily. The Rosaceae, Flacourtiaceae, Liliaceae, Euphorbiaceae, and Leguminosae are examples of heterogeneous families, and their extensive affinities are largely due to the rationale used when establishing relationships.

ANALYTICAL CIRCUMSCRIPTION OF TAXA

Davis and Heywood (1963, p. 109) discussed the formation of "dustbin groups" as being by *methodi cloacae*. In this method analysis is overemphasized in group formation. Smaller, more manageable taxa are formed by the removal of elements with distinctive characters from a larger group; common possession of "key" characters is all that is needed for membership in the new group. Thus, for example, *Agapetes* D. Don ex G. Don (and other genera) is recognized as being distinct from *Vaccinium* L., the Empetraceae as distinct from the Ericaceae, the Cuscutaceae from the Convolvulaceae, various genera from *Anemone* L. and *Thalictrum* L., and the Asclepiadaceae from the Apocynaceae. These distinct elements may be polyphyletic grade groups (e.g., *Agapetes*—note that it is taxonomically monophyletic) or strictly monophyletic groups (e.g., Cuscutaceae); the residuum is paraphyletic and has no unique, derived features restricted to it.

PRIMITIVE CHARACTERS, INTERMEDIATE TAXA, AND ANCESTORS

One of Thorne's important working principles (Thorne, 1958, 1963, 1976; see also Sargant, 1908; Turrill, 1942, including references) is the use of the primitive members of a group to establish relationships with another group—finding the nonmissing link (Cronquist, 1965; Thorne, 1974). An oft-quoted example of this is the genus *Saruma,* of the Aristolochiaceae (e.g., see Hallier, 1903; Thorne, 1963). It has an almost superior gynoecium of separate carpels, and trimerous, actinomorphic flowers. These and other largely primitive characters suggest a relationship to the Annonaceae. Primitive characters are generally considered highly important in linking groups and establishing relationships (e.g., see Dupuis, 1984). Thorne (1974) supported ideas of the relationship and immediate common origin of the members of the Annoniflorae because of the common presence of numerous primitive ancestral angiospermous features, and Endress (1977) listed a largely primitive suite of characters that occur in both the Fagaceae and the Hamamelidaceae as evidence of the relationship between the two. Monocolpate pollen grains figure prominently in the discussion of the relationship between monocotyledons and dicotyledons (e.g., see Takhtajan, 1969), but such grains also occur in the gymnosperms. Merxmüller (1977) summarized the results of a conference on evolutionary classifications almost entirely in terms of primitive characters, while Huber (1977) would have been prepared to consider an arrangement of the monocotyledons based on the similarities that they showed to dicotyledons, were it not for the reticulate affinities shown by the former. It should not be forgotten that the criteria used in determining which characters are primitive and which advanced are often suspect (for a review, see Stevens, 1980).

The principle of finding the nonmissing link has obviously been successful at times. However, there are two factors complicating its use. First, such primitive characters may be found only in the pair of taxa being compared, thus being unique to the two and useful as evidence of common ancestry. However, if they are of more general occurrence, as in the examples given above, a

relationship could equally well have been suggested with a variety of other families. The use of numerous characters may alleviate the problem, but unless these different kinds of primitive characters are distinguished, the justification for a particular relationship must be ambivalent.

Second, intermediate groups, primitive characters, and ancestors have become connected in a curious way. *Saruma* is considered to be both intermediate in position and primitive in many of its characteristics. Botanists tend to treat intermediate taxa as living fossils: taxa that link become ancestral, and their characters primitive. Although there is an element of convention in our use of terminology and "extinct ancestors" are implicit in our discussions (B. L. Burtt, pers. comm.), this is not evident in many papers. There are obviously exceptions (e.g., Burtt, 1977), and Thorne (1976), Stebbins (1976), Dahlgren (1975), and others have commented on the danger of considering ancestors to be extant, which is indeed one of the most criticized aspects of evolutionary systematics. Barabé and Brouillet (1982) distinguish between evolutionary and cladistic systematics in part because in the former the ancestors can be recognized and identified, but the point made here is that an ancestor of a particular group is often treated as being alive and/or a member of a coordinate higher taxon.

Intermediate Taxa and Gaps

Cronquist (1983) has recently emphasized what he calls McVaugh's Principle (see McVaugh, 1945, for the action of this principle at lower taxonomic levels), which facilitates the taxonomic treatment of intermediate, "ancestral" groups. A segregate taxon that is joined to another taxon by a few intermediates is maintained as a distinct and distinguishable entity by including the intermediates in the (larger) taxon in which the segregate was originally placed. The larger taxon will be more variable, some of its members perhaps already possessing the characters of the intermediate taxon because of parallel variation or convergence (see below). Thus its description will have to be changed only slightly, if at all, to accommodate variation shown by the intermediates; the description of the less-variable segregate taxon would have to be changed considerably if the intermediates were placed in it.

That taxa are commonly formed in this way may explain why characteristics rare in one group may be widely distributed in another (Thorne, 1976, principle 16, "trends or tendencies"). Thus, Cronquist (1981) noted that the Flacourtiaceae, basal in the Violales, show tendencies toward the features of several other families of that order. It also explains how the problem of the ancestor is dealt with given a belief in gradual evolution (Ashlock, 1971): the ancestor is submerged in the group from which it evolved rather than being placed with its descendants. "Ancestral groups" tend to be polythetic.

McVaugh's Principle is a special case of a more general rule whereby easily characterized groups are kept separate from the taxon from which they are supposed to have arisen. This general principle encourages the recognition of groups that are formally equivalent, having the same rank, but not otherwise comparable. The segregate may be strictly monophyletic, but the group from

which it is segregated is not.[5] Group rank is then in part determined by gap size. Huber (1977) illustrated the point: the nature of the variation shown by the monocots suggests a particular relationship to the dicots, but the rank of the monocots depends on the size of the gap between the two groups. McVaugh's Principle basically generates illusory gaps. Of course, McVaugh's Principle may be adopted simply for the sake of expediency, but the resulting classification is used as if it were in some sense real (see below). The rationale given for the use of this principle is often that gaps between major lineages will tend to be smaller because of hybridization, parallelism, and convergence (Kubitzki & Gottlieb, 1984) and so will be smaller than the gaps between taxa of lower rank (Davis, 1978). However, it has been shown above how groups may be heterogeneous because of the way in which they were formed and the way variation in them is discussed. Gaps between such groups will indeed tend to be small.

RELATIONSHIPS OF TAXA

Since taxonomic or genealogical monophyly is the concept adopted by most authors, taxa are discussed or depicted as being related—or as giving rise—to other taxa (e.g., see Hutchinson, 1973; Ehrendorfer, 1976; Takhtajan, 1980; Cronquist, 1981). As has been emphasized, many of the ways in which groups are formed encourage the production of heterogeneous, perhaps polythetic taxa. Such polythetic taxa will show a diffuse and extensive set of similarity relationships with other groups; Sokal and Sneath (1963) noted that the hierarchical relationships of such groups may be unclear. For example, the characters of a family that both distinguish it from and signify relationships with other families are classically considered to be practically all the characters in the family, whatever their actual cladistic position in the family may be (see Stafleu, 1966).

In line with the extent of the relationships shown by such groups, transections of evolutionary trees are most favored for depicting relationships (Benson, 1957; Stebbins, 1974; Sporne, e.g., 1975; Dahlgren, 1980, 1983; Dahlgren & Clifford, 1982; Behnke & Barthlott, 1983; Thorne, 1983); even treelike diagrams have become more shrubby (Heywood, 1978; Stevens, 1984b; also Rodriguez C., 1950; Dahlgren, 1975; Heywood, 1977). Since closeness of relationship—the distance between branches—depends more on the number than on the kind of characters that are held in common (Takhtajan, 1969; Heywood, 1977), taxa can readily be discussed as being intermediate between others. Discussion of particular characters of a lineage, and of lineages in general, is difficult. Finally, it is lamentable that fossils, often considered to give indisputable evidence of ancestry (see Stevens, 1980), are absent. The vertical dimension of evolutionary trees cannot be discussed.

As a result, direct relationships between groups are not drawn, but any can

[5]The pervasiveness of taxonomic monophyly in evolutionary systematics may be more apparent than real. Situations in which the "descendant" family arose from a single species in the "ancestral" family, and those in which it arose from several, are not distinguished. However, if the "descendant" family originated from a single species, it may be strictly monophyletic. The "ancestral" family may be genealogically monophyletic (paraphyletic).

be imagined. It is hardly surprising that Metcalfe (1983) observed that relationships between groups to some extent had the form of a three-dimensional reticulum, and Huber (1977) commented on the reticulum of affinities in higher monocotyledonous taxa (see Hamann, 1961; Sattler, 1977; Dahlgren & Clifford, 1982; Huber, 1982; Mabberley, 1984; see also Stevens, 1984b).

THE NATURE OF HIGHER TAXA AND ITS INFLUENCE ON GROUP FORMATION

The preceding sections may well have left the reader bemused: why has evolutionary systematics adopted its present confused and confusing position? Let me somewhat tentatively suggest one of the factors involved.

That many taxa in botany are indefinable and what are now called polythetic has been a matter of frequent comment over at least the last 230 years (Johnson, 1968; Jensen, 1983; Stevens, 1984b). Polythetic or even less-clear-cut taxa are common today. For at least 80 years evolutionary systematists have "explained" the sporadic taxonomic occurrence of characters in such groups in terms of parallelism or convergence (the latter term may be used when referring to similarities between clearly unrelated groups—Burger, 1977). This is a major concern of systematists (e.g., see Cronquist, 1957, 1981; Philipson, 1961; Takhtajan, 1969; Stebbins, 1974; Meeuse, 1975a; Thorne, 1976; Huber, 1977; Cain, 1982; Sneath, 1983; Stevens, 1984b [discussion in some detail]). The open nature of plant growth and the supposedly simple nature of plant developmental pathways and construction are explanations at another level.

The polythetic nature of these nineteenth-century taxonomic groups was in considerable part the result of the overall rather superficial level of knowledge of characters, and of the rationale used to form the groups (overall similarity—Stevens, 1984b). Such groups are also the type that would theoretically be expected, given how early-nineteenth-century botanists, in particular, visualized the world (Stevens, ms.). The continued use of overall similarity and the relatively late adoption of comparative anatomy and the like as taxonomic tools have ensured the continued production of polythetic groups: parallelisms become even more pandemic.

However, the use of forms of overall similarity to establish evolutionary relationships is also seen as a *solution* to the problem posed by parallelisms (e.g., see Davis & Heywood, 1963), although clearly it can be argued that this way of grouping helped to cause the problem in the first place. To Stebbins (1974) parallelisms were so common that individual homologies (which he considered to be structures in a group descended from the same structure in the common ancestor of that group) could not be readily recognized and so had to be subordinated to overall resemblance (not defined) when interpreting phylogenetic relationships. A similar position was expressed by Bailey (1949) in discussing the use of evidence from wood anatomy to assess relationships. To some this would seem to be the most valuable evidence available, but Bailey wisely considered that anatomical evidence—and indeed any evidence used by itself—was insufficient in placing plants in a phylogenetic sequence, although such evidence might negate a proposed arrangement (see also Davis & Hey-

wood, 1963). If attitudes such as these lead simply to the use of many putatively derived characters, that is one thing, but if they lead to the use of many characters of uncertain status, it is another. Unfortunately, the latter seems to be more frequent.

Wardlaw (1968) suggested that in the twentieth century the study of homologies became at least partly supplanted by the study of homologies of organization (parallelisms); some systematists indeed came to accept known parallelisms as evidence of relationships. It was accepted that the frequent occurrence of unusual "tendencies" in a family might help in the identification of specimens of that family (e.g., see Wagenitz, 1963); it was only a short step to the recognition of a taxon *because* of these tendencies. This reaction was not at all uncommon (cf. Rasmussen, 1982). Ideas that parallelisms might be expected if relationships were close first became current in the latter part of the nineteenth century (Vavilov, 1922; Wardlaw, 1965), and a much-cited mechanism by which this could happen was proposed by Vavilov (1922). Similar characters, but of independent origin, arose because of relationships between the taxa (cf. homiologous variation of Kubitzki & Gottlieb, 1984). Parallel variations would be likely as adaptations in related taxa to similar environmental conditions (Simpson, 1961; Joysey, 1964). Very often the use of parallelisms to suggest relationships was associated with orthogenetic ideas (Rasmussen, 1983). Wernham (1912; see Stearn, 1981) was a particularly influential author in this respect; to him, critical tendencies were often very important in establishing relationships—a character variable in the ancestor became fixed in the descendant. Wernham, at least at times (1914), adopted taxonomic monophyly, which is compatible with such notions. Cronquist (especially 1956, 1963) has also considered orthogenesis with some favor, although more recently (e.g., 1981, 1985) he has mentioned only the pattern responsible for the idea, extensive parallelism. (For other references to orthogenetic thought, see Heads, 1984; Grehan, 1984.)

Similarly, Davis and Heywood (1963, p. 41) noted that the acceptance of Corner's principle of transference of function (Corner, 1958) might lead to "resemblances between *analogous* organs [being] a better indication of affinity than resemblance in homologous ones!"; Davis and Heywood's definition of homology would probably be resemblance due to common ancestry. Certainly, invoking transference of function complicates the recognition of homology, however defined (e.g., see Berg, 1979).

Thorne (1976) favored the idea that parallelism may indicate common ancestry; he noted (1974) that the suborders of the Annonales held together in part because of common trends in specialization. To Van Steenis (1978) parallelism was a characteristic of "true affinity"; to Burger (1977) only convergences (similar characters in unrelated groups) were inadmissible as evidence of relationship. Discussion about parallelisms is generally confused (Sokal & Camin, 1965, equated parallelisms with synapomorphies) and is frequently simply circular, partly because the definition of homology is imprecise, which in turn is connected with the variety of "relationships" being discussed.

Some authors (e.g., Meeuse, 1975b, 1981; Hughes, 1977; see Stebbins, 1974, and Hickey & Doyle, 1977, for other references) suggest a polyphyletic or pleiophyletic origin of the angiosperms. Many others (e.g., Stebbins, 1974),

although rejecting independent origin from "entirely different" ancestors, allow its possibility from more closely related ones—taxonomic monophyly. Here the particular definition of monophyly adopted becomes crucial (see also Gilmour, 1940). If members of a taxon arise from a number of immediately unrelated species or higher taxa, as is permissible in taxonomic monophyly, almost the only reason why some characters are at least common in the first taxon is parallel variation (Cronquist, 1985, thinks that this is a likely evolutionary pattern, but that is beside the point here—how do we *recognize* this pattern?). Another possibility is that the "derived" group is characterized by primitive characters. Hence, if parallelisms did not occur, the different lineages would have different characters and would be readily—or more readily—separable. (Of course, if the ancestor of the derived group is included with the "ancestral group" [see discussion of McVaugh's rule] for reasons of convenience, then parallelism need not be invoked [see footnote 5].)

The idea that parallelism is in some way indicative of ancestry pervades evolutionary systematics and has been explicitly advocated by many of the most important workers in the field. Other equally influential workers, from Engler onward (see APPENDIX 2), have adopted a definition of monophyly that implicitly supports such an idea. It cannot be dismissed in any attempt to evaluate the methodology of evolutionary systematics in botany. (Cantino [1982, 1985] discusses the circumstances under which similar ideas may be of use in the recognition of cladistic relationships [but cf. Dahlgren & Rasmussen, 1983].)

Thus the indefinability of plant groups, interpreted in evolutionary terms as the ubiquity of parallelism, encourages the persisting attempts to detect evolutionary relationships by some form of overall similarity. This will lead to the recognition of more polythetic, and so indefinable, plant groups.

Fueling this attitude toward plant groups is the apparent lack of selective/adaptive or even functional significance of many characters. The literature (and terminology) dealing with such concerns is extensive (see Stevens, 1980, for some references). Wernham (1912) adopted this idea, and it has also been entertained by Cronquist (1956, 1965, 1968), Thorne (1958), Bremekamp (1962), Takhtajan (1969), Dressler (1981), Van Steenis (1981), and others. (Stebbins [1974] is a notable exception, and more recently general progress is being made in considering plant structure in terms of function.) Although practically this should have no effect on group recognition, it will make already rather nebulous groups even more so. Groups are not characterized clearly, and on top of this it is difficult to understand even the present function of those characters that do occur.

DISCUSSION

From the TABLE it can be seen that the correspondence between evolutionary and pre-Darwinian systematic practice is extensive. Throughout this discussion the interconnectedness of certain ideas of evolutionary systematics has been clear: parallelism is widespread, groups are polythetic, natural taxa are taxonomically monophyletic, and taxa can be recognized by using some variant of weighted overall similarity in homologous characters. The central role played by taxonomic monophyly, even in its less-extreme definition (see above), becomes clear. It has an appropriately evolutionary quality, and it also legitimizes

The origin of some principles of evolutionary systematics.

PRE-DARWINIAN CLASSIFICATIONS*	POST-DARWINIAN CLASSIFICATIONS	EVOLUTIONARY SIGNIFICANCE/ INTERPRETATION
Use of many features in group formation	Same	Use of unique features impossible because of parallelisms
Groups lack defining features	Same; groups polythetic at best	Parallelisms widespread
Relationships directly between groups of same rank	Same	Taxonomic monophyly: ancestor–descendant relationship between higher groups
Groups showing relationships in all directions; relationships discussed in terms of reticula, maps, etc.	Same; relationships discussed as if between branches of a transection of a tree, or members of a three- or more-dimensional array	Groups not showing unique relationships because of parallelisms (*inter alia*); fossils, perhaps able to show phylogeny, absent; phylogeny (trunks of tree) thus problematic
Natural order a continuum or not; variation perhaps continuous when more known; intermediates demonstrating principle of continuity	Ambiguity: gaps caused by extinction, but intermediates sought to help establish relationships	Groups the result of evolution; extinction enabling grouping; intermediates perhaps ancestors
Ambiguity: groups perhaps ultimately arbitrary both in rank *and* circumscription, but ± discrete groups still recognizable	Groups nonarbitrary in circumscription, if somewhat arbitrary in rank	Evolutionary interpretation of classification possible
Rank determined by size of gap between groups, also affected by group size for believers in continuity	Rank determined by size of gap between groups, also affected by group size, etc.	Time of divergence of group dependent on gap size and group rank

*For further details, see Stevens (1984b, ms.).

the taxa in pre-evolutionary classifications—their circumscription, the higher taxon–higher taxon relationships that they show, and at least by implication, the way in which they were formed. The continued production of polythetic groups is ensured. That these ideas are interconnected is only partly the result of a conscious attempt to make them so. It is also the more or less unconscious result of the continued use of the similarly interconnected principles of early-nineteenth-century systematics in the twentieth century, and their translation into evolutionary terminology (see Naef, 1919; Sokal & Sneath, 1963; Stevens, 1984a, 1984b).

This persistence also clarifies why intermediates should be ancestors, dead or alive. The principle of continuity, with intermediates between groups being

expected, was widely held in the early nineteenth century (*natura non facit saltus*—Linnaeus, 1751), and it strongly influenced a number of the most important French- and English-speaking proponents of the natural method until about 1850. Thus intermediates were expected, and when reticula were later turned sideways and called trees, the intermediates simply became ancestors. Yet later, when trees fell out of favor and onto their sides, intermediates were still discussed because ancestors could not be recognized. Ramsbottom (1938) noted the similarities between these newly felled trees and early diagrams of relationships (as in Giseke, 1792) in which intermediates played an important part.

Takhtajan (1980, p. 234) thought that phylogenetic (evolutionary) systematics had been enriched over the years by "theory, the conceptual apparatus." In fact, Cullen (1968) seems to have been somewhat nearer the mark when he observed how little discussion had been occasioned by theoretical works published in the preceding century and a half (see also Stevens, 1984b). Apart from the art and artifice used in group formation, systematics has been mistakenly considered a basically empirical—perhaps almost Baconian—discipline by which the natural order is revealed (see especially Hull, 1970, but cf. 1984); "natural groups" simply have to be recognized. Relative disinterest in theory is to be expected of a discipline that considers itself basically empirical (Reif, 1983; cf. Stevens, 1984c, and Tomlinson, 1984). As a result the real conceptual basis of the evolutionary school of systematics has been largely misunderstood, with the resultant compromise of the discipline.

Thus it is perhaps ironic that Takhtajan (1958) observed that earlier authors of evolutionary systems at most offered very weak corroboration of their views, or no substantiation at all (there are exceptions, of course). Much current documentation and justification remain unconvincing. Interpretations of the evolutionary significance of characters vary widely from author to author. The use of additional criteria that affect rank and circumscription of taxa—amount of variation contained in a taxon, size of taxon, convenience for the user, and custom (e.g., see Cronquist, 1968; Jeffrey, 1982; Ehrendorfer, 1983)—leads the user farther from an evolutionary classification, let alone a classification from which knowledge of cladistic relationships can be obtained (see also Edwards & Cavalli-Sforza, 1964; Bremer & Wanntorp, 1978; Barabé & Brouillet, 1982; Stevens, 1985). It is thus insufficient to champion the use of the hypothetico-deductive method in systematics (e.g., see Takhtajan, 1969) since some of the premises of evolutionary systematics are suspect.

There are three interconnected reasons that contribute to the relative unconcern among taxonomists about the relationship between classification and theory. First, at least some higher taxa, being "natural" (read "real") taxa, appear to have an almost unassailable ontological status. This emphasizes that one critical element in the development of evolutionary classifications (and classifications in general) is the attitude of the taxonomist toward groups established by his or her predecessors. These groups are often taken to represent "real" groups. That they are recognizable by the eye is proof of that reality; the principles used in their formation are of less importance.

This attitude is a recurring one. It is visible in Tournefort's (1694) criteria for the recognition of genera of the second rank, as well as in Linnaeus's genera

(Walters, 1961). Even Adanson (1764) used existing groups to show that no one character separated them unambiguously. Although Adanson was combating an overly a prioristic and analytic approach to classification, attitudes such as this can also be seen as protecting "natural" groups from dismemberment.

Second, the unchanging nature of taxonomic practice may seem to be evidence of its success and usefulness in science. To many there is then no necessity to change the way we analyze the world, despite our changing ideas as to the origin of diversity in that world (Walters, 1961, especially 1964). To put the argument like this cries out for an analysis of the principles of classification that is so far lacking.

Since there are no clear criteria for evaluating characters or relationships, the frequent pleas will often be heeded that systems should not be changed until we have strong evidence for, or are even "sure" of, a particular change. It is thus hardly a matter for surprise that new characters may not change the system (cf. Stafleu, 1969); new characters are evaluated in the old way. The systems are internally consistent; as M. Frohlich (pers. comm.) has emphasized, this is an important goal for most of us. They are consistent both with the primary interlocking principles of the TABLE and, more specifically, with a particular way of interpreting the data. Systems can, and indeed have, changed radically with changing opinions on "which way up" evolution is; data are reinterpreted, but using rather similar general arguments. However, the primary principles remain unaffected (see Wiley, 1979). The apparently substantial differences between the Englerian and Besseyan schools are of this relatively secondary nature.

Third is the great importance attached to nomenclatural stability, and the concomitant reluctance to change names.

A few authors (e.g., Turrill, 1957; Walters, 1961; Clayton, 1974) have commented more or less severely on the constraining effects of previous work and on what current taxa are perhaps supposed to represent. Thorne (e.g., 1976) has perhaps been most vocal in attempting to divorce present classifications from considerations of size or economic importance of taxa and also tradition (cf. Cronquist, 1968; Davis, 1978; Van Steenis, 1978). Ranking of taxa can often be traced back to decisions made over a century ago that were explicitly decisions of convenience (e.g., see Burtt, 1977; Van Steenis, 1978; Stevens, 1984b, ms.). Many systematists faced with the conflicting goals of evolutionary classifications—depicting phylogenetic relationships and promoting stability of classifications—have opted for the latter (see Stevens, 1984b, for references). It is difficult to contemplate classification without simultaneously thinking of convenience.

All three reasons reinforce the tendency to evaluate characters in terms of how they support current ideas of relationships. Thus the task of the contributors to the 1973 Amherst conference on angiosperm phylogeny was to see how the characters they were studying could be applied to the Cronquist and Takhtajan systems (Walker, 1975). Harris and Bisby (1980) see problems in being able to find evidence that conflicts with a current classification. There is perhaps less inclination to explore the taxonomic structure suggested by our

data than to confirm the existing structure (Burtt *et al.*, 1970, and Stevens, 1984b; it can be argued that the classifications are really being tested, but see above). Thus the stability that Barabé and Brouillet (1982) see as the advantage of at least some evolutionary classifications is largely attributable to the built-in resistance of such systems to change and the poor resolution of cladistic relationships that they often intentionally reflect. The supposed didactic advantages of stable classifications will prove illusory in the long run to the extent that the classifications fail to advance biological theory. Hence the agreement between evolutionary systems often mentioned (e.g., Cullen *in* Davis, 1978; Cronquist, 1981; Kubitzki & Gottlieb, 1984) seems beside the point.

I do not deny that there is a particular historical relationship between taxa, and that certain similarities between organisms are the result of their sharing a particular and unique historical relationship. However, claims that natural groups are in some sense real because they can be recognized seem to confuse perception with reality (but cf. Riedl, 1978, 1982). The word "natural" (or even "natural kind") brings along with it connotations that our fragile hypotheses about the "natural world" should not and cannot bear (see also Ghiselin, 1969, chapter 4; Desmond, 1982, chapter 6; Hull, 1983).

This all highlights the fundamentally ambiguous and ambivalent relationship between the orthodox taxonomist, the characters that he or she uses to form a group, and the groups themselves. Description of "natural" taxa becomes a prescription for the formation of similar groups: particular patterns are preferentially produced yet are described as being a common result of the evolutionary process. The taxa initially recognized seem immune from criticism and provide a pattern to which other taxa must conform. Taxonomists form groups in ways that result in recurring regularities in pattern and adopt a supporting set of definitions that incline to the same end.

In general, taxonomists learn how to form groups almost unconsciously as part of what amounts to the apprenticeship system that is our early professional life. The emphasis of that teaching is on groups and organisms; "theory" is frowned upon because of the impossibility of providing rules in the face of the pervasive exceptions. The differing claims mentioned above as to exactly what a taxonomist "naturally" does probably reflect in large part the assimilation of different experiences during a particular taxonomist's training and subsequent career.

Classifications are made to be used, so problems arise when classifications produced in one philosophic framework are used in the context of another (e.g., Cain, 1958; Patterson, 1977; Stevens, 1984b). One of the factors affecting the circumscription of groups formally recognized in classifications is convenience, and the way in which these groups are formed is in part unconcerned with or even antithetical to the idea of evolution. Yet such classifications are interpreted in phylogenetic or even cladistic terms. Taxonomists have always claimed to recognize "natural" groups (see Guédès, 1982), and although the uses to which such groups are put change with alterations in biological philosophy, many elements in the construction of classifications are part of an almost unchanging research tradition. Of course, this discussion may not matter if we have indeed been recognizing progressively more nearly strictly mono-

phyletic groups since early attempts at natural classifications in the late 1500s (e.g., Cesalpino, 1583) or before, but without knowing it (or if the phylogenetic relationships of plants are unknowable).

Despite the methodology that was used, which is perhaps not understood by most makers—let alone users—of evolutionary classifications (see also Kubitzki, 1977), and despite the goals frequently enunciated by the makers of such classifications, which are at least more accessible, evolutionary classifications have been and generally are used as if they were cladistic (Hull, 1970; cf. Dahlgren & Rasmussen, 1983). That is, they have been treated as if the circumscription and the rank of taxa depended on relative cladistic branching positions.

Stebbins (1981) analyzed characters used in recognizing families and found that gynoecial characters were more frequently used, especially in orders having an early position in the overall phylogenetic scheme. He then suggested that such characters were therefore being selected for in the early course of angiosperm evolution. Such a conclusion depends on a classification having a cladistic basis, and also one in which the main structure is not so heavily dependent on gynoecial characters. The careful analysis by Gilmartin (1981) shows some of the dangers inherent in comparing taxa at the same hierarchical level from an evolutionary perspective.

Biogeography has until recently emphasized counting numbers of families, genera, and species in different areas. Such an approach, which has predominated for close to two centuries, would be problematic even if a cladistic framework were available. When units at the same rank may be of fundamentally different kinds, the problems are immeasurably greater. Good (e.g., 1953) wisely avoided families in his computations, but even at the generic level genealogical monophyly, rather than strict monophyly, is all that is likely for many taxa (see also Joysey, 1964). Biogeographic conclusions will change depending on whether the taxa being discussed are sister groups, strictly monophyletic but not sister groups, paraphyletic, or some combination of these.

Davis (1978) commented that a formal classification is needed for the study of evolution. However, it cannot be just any classification. To understand how much divergence there has been between two members of a lineage, the cladistic relationships of the groups being compared must be established. For many of the problems of comparative biology, we have to know just what units are being compared and what their cladistic relationships are. Evolutionary systematics in places adopts a methodology that may not produce the kind of unit needed by the comparative biologist, be he or she interested in the transformation of characters through time, in the development of their functional properties or ecological relationships, or in biogeography (e.g., Bremer & Wanntorp, 1978; Funk, 1985). Kubitzki (1977, p. 25) noted that if "the sequence and position of contemporaneous groups relative to each other (without practically any knowledge of their cladistic relationship) really is the main phylogenetic/evolutionary content of such [current] classifications," then Heywood (1973) was correct in his assertion that phylogenetic schemes were based on a far-too-unscientific methodology. However, recent more or less successful at-

tempts to provide such a framework suggest lines of approach to be adopted (see especially Cantino, 1982; Dahlgren & Rasmussen, 1983; Donoghue, 1983).

A problem that has been central to our attempts to analyze relationships is our belief that many groups are polythetic. We assume this almost as an article of faith, but it may be in part an illusion reflecting our relative ignorance of our methods of analysis and knowledge of the organism; the evidential basis for this belief needs scrutiny. Interpretations of the apparent patterns and regularities in evolutionary systems, whether in terms of reticula, widespread homoplasy, or the like, are not necessarily interesting statements about patterns in the world, but they may be related very directly to the way in which we have analyzed the world.

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APPENDIX 1. **Heterobathmy.**

The problem posed by heterobathmy or "discordant" character change (Meeuse, 1975b)—greater change in one lineage than another, or only some organs changing in a lineage—is commonly of concern in evolutionary systematics. Takhtajan (1980, p. 233) outlined the problem:

> On the basis of the study of evolution of an adequate number of independent non-correlated [not logically correlated] characters belonging to a sufficient number of different high weight character complexes, we can establish the basic trends of evolution of a taxon, discover those of its members which are nearest to the phylogenetically initial forms and which are derivative, and deduce the cladistic [strict sense] relationships among orders and families of flowering plants. But in doing this we must always reckon with the phenomenon of heterobathmy.

There are a number of reasons why heterobathmy exercises authors so much. If some organs in an organism have changed and others have not, then establishing primitive character states by correlation presents problems (e.g., Stevens, 1980; Hill & Crane, 1982, p. 197, discussion of reversals). Simple differences between two lineages in amount of change may indeed not affect the establishment of cladistic relationships (Farris, 1972), but they may cause some problems in establishing levels of advancement (see Sporne, 1949), since two taxa may have the same overall level of advancement after specialization in different organs. Further, because a lineage that is cladistically not basal may evolve a great deal, its taxonomic rank will have to be raised correspondingly since rank is in part proportional to gap size. Nevertheless, taxonomic or genealogical monophyly may still be preserved, and heterobathmy in this sense is largely responsible for the main feature of evolutionary classifications, paraphyletic taxa (e.g., see Mayr, 1974). Since the amount of difference between two taxa is often considered to be proportional to the time since their divergence, heterobathmy causes major problems in the evolutionary inter-

pretation of such classifications (Davis & Heywood, 1963, including references). If the real problem is parallel evolution, this is another matter; parallelism causes problems in the associated (or identical) phenomenon of mosaic evolution (Mayr, 1974). Both parallelisms and reversals lead to groups being polythetic.

Appendix 2. **Engler, Hallier, and Monophyly.**

To Engler (1897, principle 9) both genetic development (patristic differences?) and morphological gradation (overall level of advancement) were to be expressed in classification. Thus, although both principles 13 and 19 suggest that groups that are simply levels of organization are not to be encouraged, in direct contradiction Engler (1897, p. 368) also noted that the Parietales were not "ein einheitlicher [uniform] monophyletischer Verwandschaftskreis," but in part a group that "von verschiedenen Anfangspunkten ausgehend in ihrer Entwickelung auf derselben morphologischen Hauptstufe Halt gemachte haben" (whole passage emphasized in original). Thus taxonomic monophyly was adequate for group recognition. Some taxa, at least, were barely even grades or levels (Stufe) of organization; it was implied that the Parietales were some kind of monophyletic group, although not a uniform one.

Hallier, on the other hand, was less ambiguous about what he wanted to do. He wished his system to express natural affinities—that is, to show the genealogical tree (Hallier, 1912): "Die Rekonstruktion dieses natürlichen Stammbaums muss das Endziel der systematischen Ontologie sein" (Hallier, 1902, p. 10). Hallier (e.g., 1901) considered that Engler recognized polyphyletic groups. To Hallier natural groups were necessarily (close to genealogically) monophyletic, so they did not have to contain all the descendants of an ancestral species, as a glance at his phylogenetic diagrams shows (e.g., see Hallier, 1912); taxa are connected serially. However, taxa could not arise from a number of separate lineages, and this was the basis of his argument with Fritsch (1905; Hallier, 1905), representing the Englerian school, who thought that the anthophytes (flowering plants) had two separate origins in the gymnosperms.

A REVISION OF PSYCHOTRIA (RUBIACEAE) IN SAMOA

W. A. WHISTLER[1]

The family Rubiaceae is one of the largest of all angiosperm families and is particularly abundant in the tropics. In Polynesia it comprises 24 genera (Darwin, 1979) and in species numbers is probably the largest dicotyledonous family. *Psychotria* L. is the largest of the Pacific genera of Rubiaceae and is perhaps second only to *Cyrtandra* J. R. & G. Forster of the Gesneriaceae in the number of native species in the region. *Psychotria* has fruits and seeds that are readily spread by frugivorous birds and is prone to speciation when dispersed to new areas. It is found on all the major high islands of Polynesia, with about 80 species in Fiji (Darwin, 1979), 11 in Hawaii (Sohmer, 1977), nine in the Marquesas (Fosberg, 1939), and more than eight in the Society and Tubuai Islands (Fosberg, 1937). Most Pacific species of *Psychotria* are restricted to a single island or archipelago but are closely related to those of neighboring ones.

TAXONOMIC HISTORY OF THE GENUS IN SAMOA

Twenty-four species of *Psychotria* have been described from or attributed to Samoa since the first records of the Samoan Rubiaceae were published by Gray in 1860, and two other species originally described in different genera actually belong to *Psychotria.* However, since no comprehensive study of the genus in Samoa has been done and no keys have been published, the genus has long been in need of revision.

The first specimens of *Psychotria* recorded from Samoa were collected by the United States Exploring Expedition in 1839. Unfortunately, these collections were very poorly prepared—no collection numbers or localities were recorded. Twenty-one years later, Gray (1860) described five species (one of them in a different genus) based on those collections, but another 38 years passed before any more were published. During this long interval, however, several collectors were at work, most notably Graeffe (ca. 1862), Powell (ca. 1860–1870), and Whitmee (ca. 1875), but their specimens, including eight representing species new to science, were ignored until the end of the century.

The next treatment of the genus in Samoa was done by Schumann in Reinecke's *Die Flora der Samoa-Inseln* (1898). Based upon the collections of Reinecke and Graeffe, Schumann named eight new species in the genus (one, however, turned out to be conspecific with one described by Gray). Reinecke

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worked in Samoa from 1893 to 1895 and collected 13 of the 20 species that are recognized in the present paper.

After a brief hiatus, botanical work in Samoa intensified, reaching its high point in 1905, when four botanists were collecting in the archipelago. The most prolific of the four was Rechinger, who collected nearly 2000 specimens in a single four-month period, including about 15 species of *Psychotria*. From these Rechinger (1908, 1909) named four new species; three of the names, however, have now been reduced to synonymy. For some reason the fourth, still valid species was omitted when Rechinger published his collection data (1910).

Of nearly equal importance are the specimens of Vaupel, who collected in Samoa from 1904 to 1906. His gatherings included 11 species of *Psychotria*, two of which had not previously been collected. One of these was named by Lauterbach (1908) but was incorrectly placed in the genus *Randia*; the other has not been described until now. The remaining two botanists collecting in Samoa in 1905, Hochreutiner and Lloyd, did not collect any new *Psychotria* species. Their collections are of minor importance, although Hochreutiner (1934) did describe three minor varieties (which are not recognized in the present paper).

The most complete work on the genus in Samoa, and the last until the present paper, was prepared by Christophersen based upon the large collection he amassed during field work in 1929 and 1931. Christophersen collected 17 of the 20 species recognized here, two of them new to science. In his publication (1938) he named four new species, but two of the names are herein reduced to synonymy.

During field work in Samoa between 1971 and the present, I have collected over 4500 specimens, including 18 of the 20 *Psychotria* species, but none of the 18 is new. Collections by Bristol in 1968 and Cox over the last several years have likewise failed to include any new species. It thus appears that the available specimens (over 480 collection numbers) represent a fairly complete sampling of the genus, and very few new species can be expected to turn up in the future. Although the collections appear to be adequate, the study of the genus certainly is not—I have found it necessary to describe four new species and make two new combinations from the available material.

During my study of the genus, which began in 1973, I visited a number of European and American institutions to examine their collections and select specimens that were subsequently to be received on loan. Effort was made to examine and record every specimen collected in the archipelago. Specimens at the following institutions were utilized: Harvard University Herbaria (A and GH), Botanisches Museum of Berlin-Dahlem (B), Bernice P. Bishop Museum (BISH), British Museum (Natural History) (BM), Royal Botanic Garden, Edinburgh (E), Conservatoire Botanique, Geneva (G), Hamburg Institut für Allgemeine Botanik (HBG), Royal Botanic Gardens, Kew (K), Botanische Staatssammlung, Munich (M), National Herbarium of Victoria (MEL), my personal collection at the Pacific Tropical Botanical Garden (PTBG), University of California, Berkeley (UC), U. S. National Herbarium (US), Botanical Institute, Wroclaw (WRSL), and Naturhistorisches Museum, Vienna (W).

Psychotria L. Syst. Nat. ed. 10. 929, 1364. 1759, nom. cons.

Shrubs to small or occasionally medium-sized trees. Stipules interpetiolar, often connate and sometimes forming campanulate sheath, caducous. Leaves opposite or rarely appearing whorled at ends of branches, usually glabrous. Inflorescences generally terminal but occasionally in upper axils, usually paniculate and many flowered, sometimes trichotomous from base. Calyx synsepalous, lobed to subentire, 4- or 5-merous; corolla sympetalous, usually with narrow tube and 4- or 5-lobed, spreading or recurved limb, white to greenish, often pubescent within; stamens 4 or 5, epipetalous, subsessile or with short filaments, exserted or included; ovary inferior, 2-locular, each with single basal ovule. Fruits with or without persistent calyx, fleshy, red, pink, or purple at maturity, each containing 2 thick-walled, usually longitudinally ribbed pyrenes.

The genus in Samoa consists of 20 species, of which seventeen are endemic and one has two subspecies. The three nonendemic species are *Psychotria insularum* A. Gray (found in Tonga, Wallis and Futuna, and Niue), *P. forsteriana* A. Gray (Tonga, Fiji, and probably westward into Melanesia), and *P. carnea* (Forster f.) A. C. Smith (Tonga and Fiji). The distribution of the species in Samoa is shown in the TABLE. Savaii, the largest island in the archipelago, has 17 of the species, Upolu has 14, and Tutuila and the three islands of Manua have only three species among them.

Only one section of the genus, sect. *Eumachia* (DC.) A. C. Smith, has been described from the area (Fiji) (Smith, 1936), and its type species, *Psychotria carnea,* is also found in Samoa. At least four other Samoan species, *P. chlorocalyx* Schumann, *P. geminodens* Reinecke, *P. savaiiensis* Rech., and *P. vaupelii* Whistler, fit into this section, which is characterized by four-merous flowers with the corolla lobes developing edge to edge so as to give the corolla a four-angled, distally enlarged appearance before anthesis. Additionally, *P. sclerocarpa* Whistler may belong here, but the available specimens all lack flowers.

A second group includes only two species, *Psychotria forsteriana* and *P. samoana.* These differ from all other Samoan species of *Psychotria* in having two-lobed fruits with pyrenes entirely unribbed. Additionally, the flowers of these two species are the smallest of any *Psychotria* in Samoa.

A third group includes *Psychotria apodantha* A. Gray, *P. christophersenii* Whistler, *P. garberiana* Christoph., *P. insularum* A. Gray, *P. pacifica* Schumann, *P. reineckei* Schumann, and *P. xanthochlora* Schumann. These are characterized by five-merous flowers usually villous within, prominently ribbed pyrenes, and leaves that often dry mottled reddish brown and gray. Also questionably included in this group are *P. gigantopus* Schumann and *P. closterocarpa* A. Gray.

The remaining three species, *Psychotria bristolii* Whistler, *P. grandistipulata* (Lauterb.) Whistler, and *P. juddii* Christoph., do not appear to be closely related either to each other or to the three above-mentioned groups.

I hesitate to label these groups, except for the previously described sect. *Eumachia,* as sections. In his ongoing *Flora Vitiensis Nova,* A. C. Smith will soon be publishing a treatment of the approximately 80 Fijian species of *Psy-*

Distribution of Samoan taxa of Psychotria.

TAXON		ISLAND				
		Savaii	**Upolu**	**Tutuila**	**Manua**	**Other**
P. apodantha		x	x			
P. bristolii		x				
P. carnea subsp. *carnea*		x				x
subsp. *oncocarpa*			x			
P. chlorocalyx			x			
P. christophersenii		x				
P. closterocarpa		x	x			
P. forsteriana		x	x	x		x
P. garberiana					x	
P. geminodens			x			
P. gigantopus		x	x			
P. grandistipulata		x	x			
P. insularum		x	x	x	x	x
P. juddii		x				
P. pacifica		x	x			
P. reineckei		x	x			
P. samoana		x	x			
P. savaiiensis		x	x			
P. sclerocarpa		x				
P. vaupelii		x				
P. xanthochlora		x	x			
Total taxa	21	17	14	2	2	3

chotria. Since most Samoan species of the genus are undoubtedly related to the Fijian ones, it does not seem wise to assign the Samoan species to sections until the species from the two areas have been compared.

Unlike the situation described by Sohmer (1977) in Hawaii, where all the present species of *Psychotria* evolved from two or three founding species, the Samoan taxa probably owe their origin to several arrivals. Thus it is nearly impossible to discuss phylogeny of the Samoan species without studying the genus over its entire region.

Since the Samoan species undoubtedly have a multiple origin with little sign of local speciation, it is not surprising that, although there are far more *Psychotria* species in Samoa than anywhere else in Polynesia, they do not constitute a "taxonomist's nightmare" as they do elsewhere (Sohmer, 1977, p. 103). With the exception of *P. insularum* and *P. pacifica,* the genus has caused taxonomists very little trouble—only six of the twenty species, in fact, have synonyms. Most of the fertile specimens I examined were easily identifiable to species. Two of them, however, appear to be hybrids; these are discussed under *P. vaupelii.* Two other specimens appear to belong to an undescribed species, but since the material is inadequate, they are merely mentioned at the end of this treatment under "Undetermined Species." It thus appears that the need for revising the genus was not due to its difficulty but to sheer neglect.

Characters Useful in Distinguishing among Samoan Species of Psychotria

Stipules. The stipules are extremely variable in size and shape, ranging from small, linear-lanceolate ones in *Psychotria insularum* to large, persistent, campanulate stipule sheaths in *P. grandistipulata.* Sometimes even sterile specimens of apparently closely related species such as *P. insularum* and *P. xanthochlora,* and *P. christophersenii* and *P. garberiana,* can be distinguished by the stipules alone.

Leaves. Some closely related species have similarly shaped leaves that differ in petiole length. In other species, such as *Psychotria forsteriana* and *P. samoana,* the leaves are similarly shaped but differ in width.

Inflorescences. The inflorescences vary in size, degree of branching, and (in at least one case) position of origin. The closely related *Psychotria apodantha* and *P. pacifica,* for example, are most easily distinguished by such criteria: the former species has a single sessile umbel, the latter a panicle of umbels.

Flowers. The most obvious difference in the flowers is the number of parts, and sect. *Eumachia* can be separated from the rest of the Samoan species on the basis of its four- (rather than five-)merous flowers. The degree of lobing of the calyx is important in identifying one species, and the sizes of both the corolla and the calyx are significant in distinguishing many others. Several species have greenish rather than the normal white corollas, and one species even has a white calyx.

Fruits. The most important differences are in size and shape. Also significant are the presence or absence of a persistent calyx, and the presence and degree of ribbing of the pyrenes. Two species, *Psychotria forsteriana* and *P. samoana,* completely lack ribbing. Red is the normal color of the mature fruit, but three species have pink to flesh-colored fruits, and another often has purple ones.

Key to the Species of Psychotria in Samoa

1. Fruits 2-lobed, not longitudinally ribbed when dry; flowers 2.5–6 mm long.
   2. Leaves usually 1–3 cm wide; inflorescences 1–2.5 cm long, 10- to 20-flowered. ..... 1. *P. samoana.*
   2. Leaves usually 3.5–7 cm wide; inflorescences 2–6 cm long, 20- to 100-flowered. ..... 2. *P. forsteriana.*
1. Fruits not 2-lobed, commonly longitudinally ribbed when dry; flowers more than 6 mm long.
   3. Flowers 4-merous, the corolla 4-lobed, lobes reflexed after anthesis.
      4. Calyx distinctly 2-lobed. ..... 3. *P. geminodens.*
      4. Calyx 4-lobed to subentire.
         5. Fruits 16–30 mm long; corolla usually white; inflorescences 2–4 cm long.
            6. Leaves subsessile, petiole less than 1 cm long; fruits longitudinally ribbed when dry. ..... 4. *P. savaiiensis.*
            6. Leaves with petiole 2–4 cm long; fruits not longitudinally ribbed when dry. ..... 5. *P. sclerocarpa.*
         5. Fruits 10–16 mm long; corolla usually greenish; inflorescences 3–15 cm long.

7. Calyx cleft more than halfway; leaves 1.5–5.5 cm wide.
   8. Leaves 2–4 times as long as wide; Upolu. . . . . 6. *P. chlorocalyx.*
   8. Leaves 4–7 times as long as wide; Savaii. . . . . 7. *P. vaupelii.*
7. Calyx shallowly cleft; leaves 4–13 cm wide.
   9. Leaves with blade obovate, 12–22 by 7–13 cm; fruits with calyx 5–7 mm wide; Savaii. . . . . 8a. *P. carnea* subsp. *carnea.*
   9. Leaves with blade elliptic, 4–16 by 4–8 cm; fruits with calyx 3–5 mm wide; Upolu. . . . . 8b. *P. carnea* subsp. *oncocarpa.*

3. Flowers usually 5-merous, corolla never lobed.
   10. Inflorescences 10–40 cm long; leaves 14–45 cm long; fruits usually 15–35 mm long.
      11. Leaves appearing whorled at branch ends, petiole less than 2 cm long. . . . . 12. *P. gigantopus.*
      11. Leaves clearly opposite, petiole 4–9 cm long.
         12. Flowers 30–55 mm long; fruits 20–33 mm long, with single prominent rib on each pyrene face. . . . . 9. *P. bristolii.*
         12. Flowers 25–30 mm long; fruits 15–20 mm long, with several longitudinal ribs on each pyrene face. . . . . 13. *P. closterocarpa.*
   10. Inflorescences 1–10 cm long; leaves usually less than 15 cm long; fruits usually less than 16 mm long.
      13. Fruits 25–45 mm long; leaves not usually drying mottled.
         14. Flowers sessile, in many-flowered, globose heads. . . 11. *P. juddii.*
         14. Flowers on pedicels 3–20 mm long, in 10- to 20-flowered panicles. . . . . 10. *P. grandistipulata.*
      13. Fruits 7–20 mm long; leaves often drying mottled.
         15. Flowers subsessile; young stems often covered with erect, reddish brown hairs.
            16. Inflorescences panicles of umbels; leaves 20–60(–90) mm wide. . . . . 14. *P. pacifica.*
            16. Inflorescences single, sessile umbels; leaves 8–30 mm wide. . . . . 15. *P. apodantha.*
         15. Flowers pedicellate; young stems only rarely covered with erect, reddish brown hairs.
            17. Calyx 5–9 mm long, white, lobes oblong. . . . 16. *P. reineckei.*
            17. Calyx less than 5 mm long, green, shallowly lobed.
               18. Flowers 20–50 mm long; fruits 13–20 mm long, with cup-shaped calyx 2–3 mm long.
                  19. Stipules 8–16 mm long, notched at apex; fruits ovoid to subglobose; flowers up to 27 mm long; Manua. . . . . 17. *P. garberiana.*
                  19. Stipules 15–25 mm long, unnotched; fruits ovoid and often curved; flowers over 28 mm long; Savaii. . . . . 18. *P. christophersenii.*
               18. Flowers 6–26 mm long; fruits 7–13 mm long, with minute calyx.
                  20. Stipules ovate to elliptic; flowers 10–20 mm long. . . . . 19. *P. xanthochlora.*
                  20. Stipules linear-lanceolate; flowers 6–12 mm long. . . . . 20. *P. insularum.*

1. **Psychotria samoana** Schumann, Bot. Jahrb. Syst. **25:** 685. 1898; Rech. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **85:** 199. 1910; Christoph. Bernice P. Bishop Mus. Bull. **154:** 58. 1938. Var. *typica*

Hochr. Candollea **5:** 268. 1934. TYPE: Samoa, Savaii, Aopo, *Reinecke 418* (lectotype, here designated, BISH!; isolectotype, G!).

Psychotria samoana var. *microphylla* Rech. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **85:** 199. 1910. TYPE: Samoa, Upolu, near Tiavi, 1905, *Rechinger 5270* (holotype, W).

Shrub or small tree 1–3 m tall. Stems glabrous; stipules linear or lanceolate with long-attenuate tip, connate at base, 7–15 mm long. Leaves with petiole 3–16 mm long, glabrous; blade lanceolate to narrowly elliptic, 5–12 cm by 9–30 mm, the apex attenuate, the base acute, the surfaces glabrous, glossy green when fresh. Inflorescences terminal, few-branched panicles 1–2.5 cm long, bearing 10 to 20 flowers. Flowers with pedicel 0.5–2 mm long; calyx shallowly cup shaped, 1–2 mm long, entire or divided into 5 shallow, rounded lobes; corolla campanulate, 2.5–4.5 mm long, divided about halfway into 5 ovate lobes, white, glabrous outside, densely pubescent within; stamens 5, anther oblong, ca. 1 mm long, subsessile; style ca. 2–3 mm long, bifid ca. halfway into stigma lobes. Fruits obovoid to subglobose, 6–10 mm long, red at maturity, shallowly 2-lobed when dry.

TYPIFICATION. *Reinecke 304* and *418* were cited by Schumann in his description of the species. Christophersen noted the presence of *304* at B, but this and *418,* which was probably also there, were presumably destroyed during World War II. However, duplicates of *Reinecke 418* are at BISH and G, and those of *304* are at G, E, and US. I have chosen *Reinecke 418* (BISH) as the lectotype. Rechinger's var. *microphylla* is based on his *5270,* but I do not consider this specimen sufficiently different from the species to rank as a variety.

DISTRIBUTION. Endemic to Savaii and Upolu; understory tree in coastal to montane forest; near sea level to 1000 m alt.

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** SAVAII: above Aopo, *Bristol 2128* (BISH, GH, K); above Gataivai, *Bristol 2288* (BISH, GH); above Salailua, *Bryan 175* (BISH, GH); Salailua-Lataitai, *Christophersen 2871* (BISH); Siuvao-Auala, *Christophersen 3377* (BISH); *sine loco, Graeffe 145* (HBG), *206a* (HBG); near Aopo, *Rechinger 1942* (W); Ologogo, *Vaupel 639* (B, BISH, M, PTBG); E of Falealupo, *Whistler 1025* (PTBG, US); above Aopo, *Whistler 1707* (B, BISH, K, PTBG, US); above Asau, *Whistler 1768* (B, BISH, BM, K, PTBG, US). UPOLU: Malololelei-Lanotoo, *Christophersen 44* (A, BISH, K, US); *sine loco, Funk s.n.* (BM); *sine loco, Graeffe 201* (HBG); Lanotoo, *Hochreutiner 3272* (G); Tiavi, *Rechinger 456* (W), *5270* (W); Lanotoo, *Rechinger 1841* (BM, W); "Kammgebiet," *Reinecke 304* (E, G, US); Mt. Fiamoe, *Whistler 1166* (PTBG, US); Lanoataata, *Whistler 1489* (PTBG); Lepue, *Whistler 4183* (BISH, PTBG). WITHOUT FURTHER LOCALITY: *Horne 43* (GH, K), *Powell 180* (K), *U. S. Expl. Exped. s.n.* (GH, US *77357,* US *653893*), *Whitmee 145* (K).

Psychotria samoana is closely related to the more widely distributed *P. forsteriana* but differs in having narrower, often attenuate-tipped leaves and fewer-flowered inflorescences. It appears to be more closely related to *P. amoena* A. C. Smith, a Fijian endemic. The label on *U. S. Expl. Exped. s.n.* (US *653893*) indicates the locality as New Zealand, but this is almost certainly another example of the problems encountered when dealing with the improperly handled specimens from this expedition.

2. **Psychotria forsteriana** A. Gray, Proc. Amer. Acad. Arts **4:** 44. 1860; Schumann, Bot. Jahrb. Syst. **25:** 688. 1898; Rech. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **85:** 202. 1910; Hochr. Candollea **5:** 268. 1934; Christoph. Bernice P. Bishop Mus. Bull. **154:** 51. 1938. TYPE: Samoa, without further locality, *U. S. Expl. Exped. s.n.* (lectotype, here designated, US *62339*!; isolectotype, GH!).

Small tree 1.5–4 m tall. Stems glabrous; stipules lanceolate, connate on lower portion, up to 20 mm long. Leaves with petiole 0.8–5 cm long, glabrous; blade elliptic, 6–22 by 3.5–7 cm, apex acute to acuminate, base acute, surfaces glabrous. Inflorescences panicles 2–6 cm long, often branching near base, bearing 20 to 100 or more flowers. Flowers with pedicel up to 1.5 mm long, glabrous; calyx shallowly cup shaped to campanulate, 0.5–1.5 mm long, shallowly 5-lobed; corolla campanulate, 4–6 mm long, divided about ⅓ of its length into 5 spreading, ovate lobes, white, densely pilose in band below sinuses; stamens 5, epipetalous in band of hairs, nearly exserted at corolla sinuses, the anther oblong, ca. 1 mm long, the filament of similar length; style ca. 2.5–4 mm long, stigma lobes 0.5–1 mm long. Fruits subglobose to obovate, 6–12 mm long, red at maturity, 2-lobed when dry.

TYPIFICATION. *Psychotria forsteriana* was described based on specimens collected by the U. S. Exploring Expedition and was attributed by Gray to Tahiti, Samoa, and Fiji (with var. *vitiensis* A. Gray from the latter archipelago). Gray also added a questionable synonym of "*Psychotria asiatica* Forst. Prodr. p. 16? non L.," which would be a later homonym if it is the same species as *P. forsteriana.* It is not known why Gray added this synonym, and Forster's description of *P. asiatica,* "stipulus emarginatus, foliis lanceolato-ovatis," gives no clue as to why Gray would hesitantly equate the two species. Although there is a U. S. Exploring Expedition specimen of *P. forsteriana* at GH labeled as being from Tahiti, the species has never been collected there again, and it is likely that the specimen is mislabeled, an occurrence not unique among the Expedition's collections, as was noted under the above species. Two other specimens of the Expedition exist, an unnumbered sheet at GH and US *62339.* I have chosen the US specimen as the lectotype, and the GH specimen as the isolectotype.[2]

DISTRIBUTION. Indigenous to Savaii, Upolu, and Tutuila; understory tree in coastal to montane forest; near sea level to 1000 m alt. It also occurs in Fiji (var. *vitiensis* A. Gray), and in Tonga on Eua (G. Buelow, pers. comm.), but the record from Tahiti is doubtful.

ADDITIONAL SPECIMENS EXAMINED. **Samoa**. SAVAII: above Patamea, *Bristol 2328* (GH), *2329* (BISH); above Salailua, *Bryan 180* (BISH, GH, K); near Vaipouli, *Christophersen 1842*

[2]In most taxonomic literature lectotypes have been designated from United States Exploring Expedition specimens at US. Gray returned the first set to US and kept a nearly complete, but partially fragmentary, set at GH. Although some species are better represented at GH, this is not the case with Samoan species of *Psychotria.* I have therefore followed the convention of designating the US specimens as lectotypes.

(A, BISH, K, US, W); Sili, *Christophersen 3200* (BISH); Salelologa, *Cox 101* (BISH, GH); behind Sasina, *Cox 242* (BISH, GH), *260* (BISH, GH); *sine loco, Graeffe 144, pro parte* (HBG), *216, pro parte* (HBG), *217* (HBG), *220* (HBG); Patamea, *Rechinger 1142* (W); various localities, *Vaupel 11* (B, BISH, K, M, PTBG, US, WRSL); *sine loco, Vaupel 11a* (WRSL); behind Matautu, *Vaupel 666* (B, BISH); behind Safai, *Vaupel 677* (B); above Matavanu, *Vaupel s.n.* (PTBG); above Asau, *Whistler 899* (B, BISH, K, PTBG, US); near Salelologa, *Whistler 1215* (BISH, PTBG, US); above Asau, *Whistler 1762* (PTBG). UPOLU: Mt. Vaea, *Christophersen 452* (BISH, US); above Saluafata, *Christophersen 539* (BISH), *541* (BISH); above Tafatafa, *Cox 371* (BISH, GH, K); Moamoa, *Eames 188* (BISH, K), *189* (BISH, GH); *sine loco, Funk 196* (WRSL (fragment)); *sine loco, Graeffe 37* (HBG), *37a* (HBG), *90* (HBG), *212, pro parte* (HBG), *213* (HBG), *1412* (K); near Apia, *Hochreutiner 3217* (G); Papaseea, *Hochreutiner 3229* (G, GH); Tiavi, *Rechinger 374* (W), *406* (W); Laulii, *Rechinger 895* (K), *899* (BM, US, W); above Motootua, *Rechinger 1232* (BM, K, W); Mt. Vaea, *Rechinger 1393* (W); near Malifa, *Rechinger 1400* (W); near Utumapu, *Rechinger 1532* (US); Mt. Vaea, *Reinecke 152* (G, US (*pro parte*), WRSL); Utumapu, *Whistler 670* (BISH, PTBG, US), *676* (B, BM, PTBG, US); Mt. Mariota, *Whistler 754* (PTBG, US); above Luatuanuu, *Whistler 1604* (B, BISH, PTBG), *1636* (B, BISH, K, PTBG, US); Mt. Tafuaupolu, *Whistler 1665* (BISH, K, PTBG, US); near Amaile, *Whistler 1836* (B, BISH, K, PTBG, US); below Utumapu, *Whistler 1992* (B, BISH, K, PTBG); Taitoelau-Sigaele, *Whistler 2038* (B, BISH, PTBG); above Apia, *Wilder 80* (BISH). TUTUILA: Aua-Afono, *Garber 841* (BISH); *sine loco, Graeffe 37b* (H), *s.n.* (K); Pago Pago, *Meebold 8253* (BISH, K); Aoloaufou, *Whistler 2730* (BISH, G, PTBG). WITHOUT FURTHER LOCALITY: *Graeffe 173* (BM), *s.n.* (BM); *Kramer s.n.* (WRSL (fragment)); *Powell 235* (K); *Whitmee 66* (MEL), *167* (K, MEL), *s.n.* (BM, GH).

This species is very similar to the endemic *Psychotria samoana,* from which it differs principally in having larger leaves and inflorescences with more flowers. *Psychotria forsteriana* is one of the commonest of the *Psychotria* species in Samoa, perhaps second only to *P. insularum.*

Reinecke 383, collected on Mt. Fao, Upolu, could not be located and is probably lost.

3. **Psychotria geminodens** Schumann, Bot. Jahrb. Syst. **25:** 688. 1898; Rech. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **85:** 202. 1910; Christoph. Bernice P. Bishop Mus. Bull. **154:** 52. 1938. LECTOTYPE (here designated): Samoa, Upolu, Lepua [Lepue?], *Reinecke 636* (G!).

Small tree 2–6 m tall. Stems glabrous; stipules lanceolate, acuminate, connate over half their length, 10–20 mm long. Leaves with petiole 4–18 mm long, glabrous; blade obovate to elliptic, 6–16 by 3–9 cm, apex acuminate to nearly rounded, base acute to attenuate, surfaces glabrous. Inflorescences terminal, many-flowered panicles 1.5–8 cm long, divided at base into 2 to 6 branches. Flowers with pedicel 2–5 mm long, glabrous; calyx campanulate, divided about halfway into 2 lobes, glabrous; corolla salverform, with tube 10–14 mm long and 4 lanceolate to ovate, recurved lobes 8–12 mm long that give upper portion of corolla distinctly 4-ribbed appearance before anthesis, green; stamens 4, epipetalous and partly exserted at top of tube, the anther linear-oblong, 3–4 mm long, the filament ca. ½ as long as anther; style shorter than tube, included, stigma lobes ca. 1 mm long. Fruits obovoid, 13–17 mm long excluding persistent, 2-lobed calyx 3.5–5.5 mm long, red at maturity. $n = 11$ (*Whistler 1575*).

DISTRIBUTION. Endemic to Upolu; understory tree in foothill and montane forest; 200–800 m alt.

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** UPOLU: above Malololelei, *Christophersen 259* (A, BISH); Lanotoo, *Rechinger 762* (W), *1834* (W); Utumapu, *Whistler 684* (BM, PTBG, US); Mt. Fiamoe, *Whistler 1175* (B, BISH, K, PTBG, US); Lanoataata, *Whistler 1505* (BISH, PTBG, US); Afulilo, *Whistler 1575* (BISH, K, PTBG); above Luatuanuu, *Whistler 1603* (B, BISH, PTBG); Lanotoo, *Whistler 2172* (PTBG); Olomaga, *Whistler 3884* (PTBG); above Togitogiga, *Whistler 3910* (BISH, PTBG, US).

This is the only species of the genus in Samoa to have a 2-lobed calyx. Its flowers are similar to those of the other 4-merous species of *Psychotria,* and it is probably related to them.

4. **Psychotria savaiiensis** Rech. Feddes Repert. Spec. Nov. Regni Veg. **6:** 327. 1909. TYPE: Samoa, Savaii, near Maugaafi, 1905, *Rechinger 690* (holotype, W!).

Calycodendron(?) sp. of Christoph. Bernice P. Bishop Mus. Bull. **154:** 64. 1938.

Small tree 1.5–4 m tall. Stems glabrous; stipules acute-tipped, connate over half their length, 8–16 mm long. Leaves with petiole 4–8 mm long, glabrous; blade obovate to elliptic, 20–30 by 8–16 cm, apex acuminate to cuspidate, base acute, surfaces glabrous. Inflorescences compact, short-stalked panicles from upper axils, 2–4 cm long, bearing 10 to 20 flowers. Flowers with pedicel 2–6 mm long, glabrous; calyx campanulate, 6–9 mm long, divided about ⅓ of its length into 4 acute lobes; corolla salverform with narrow tube 12–18 mm long and 4 elliptic to ovate, spreading to recurved lobes 8–12 mm long that give upper portion of corolla distinctly 4-ribbed appearance before anthesis, white; stamens 4, epipetalous in upper throat, partially exserted, the anther subsessile, linear, 7–9 mm long; style included, about ½ as long as corolla, stigma lobes 1–2 mm long. Fruits ellipsoid to obovoid, 15–30 mm long excluding persistent cuplike calyx, red to purple at maturity, longitudinally ribbed when dry.

DISTRIBUTION. Endemic to Savaii and Upolu; understory tree in montane forest; 500–800 m alt.

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** SAVAII: above Salailua, *Christophersen 2743* (BISH, PTBG); Siuvao-Auala, *Christophersen 3289* (BISH); above Asau, *Whistler 14* (BISH, PTBG), *896* (PTBG), *1745* (B, BISH, BM, K, PTBG, US). UPOLU: Mt. Sigaele, *Whistler 2052* (PTBG).

Rechinger described this species in 1909 but omitted it from his 1910 work. Christophersen collected it twice but, unaware that Rechinger had already described it, tentatively referred it to *Calycodendron.* However, both Fosberg (1941) and Darwin (1979) believed this genus to be indistinct from *Psychotria,* and Rechinger's name must stand. Even if *Calycodendron* were to be considered a distinct genus, *P. savaiiensis* would be unaffected since this species is more closely related to section *Eumachia* than it is to *Calycodendron* (A. C. Smith, pers. comm.).

5. **Psychotria sclerocarpa** Whistler, sp. nov.

?*Psychotria* sp. of Schumann, Bot. Jahrb. Syst. **25:** 689. 1898.
Psychotria sp. of Rech. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **85:** 203. 1910.

Differt a P. carnea fructu majore et calyce quasi integro longiore.

Small tree up to 6 m or more tall. Stems glabrous; stipules not seen. Leaves with petiole 2–4 cm long, glabrous; blade obovate, 12–24 by 7–13 cm, apex acuminate, base acute to cuneate, surfaces glabrous. Inflorescences terminal, few-flowered panicles 2–6 cm long, branching at base. Flowers with pedicel 2–6 mm long, glabrous; calyx campanulate, 6–8 mm long, subentire to irregularly serrate; corolla, stamens, and style not seen. Fruits ovoid, 15–20 mm long excluding persistent calyx, not obviously transversely ribbed when dry.

TYPE: Samoa, Savaii, above Ologogo, *Whistler 580* (holotype, PTBG!; isotypes, B!, K!, US!).

DISTRIBUTION. Endemic to Samoa (Savaii and possibly Upolu); understory tree in montane forest; ca. 700 m alt.

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** SAVAII: *sine loco, Graeffe 1507* (HBG); near Matavanu, *Rechinger 3737* (W).

This species is very rare, having been collected only three or four times and never with flowers. Nevertheless, it probably belongs to section *Eumachia* and has four-merous flowers with the corolla ribbed prior to anthesis; it was placed in the key to species based on this assumption. *Psychotria sclerocarpa* is similar to *P. carnea* but differs in having a larger, subentire calyx and larger fruits. *Reinecke 142* (BISH, G), collected at Alofau on Upolu, appears to belong here; if so, the species occurs on both Savaii and Upolu. The epithet *sclerocarpa* was taken from an annotation on *Rechinger 3737,* but the species was never described.

6. **Psychotria chlorocalyx** Schumann, Bot. Jahrb. Syst. **25:** 688. 1898; Rech. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **85:** 202. 1910; Christoph. Bernice P. Bishop Mus. Bull. **154:** 50. 1938, *pro parte.* TYPE: Samoa, Upolu, Le Pua [Lepue?], *Reinecke 635* (lectotype, here designated, G!; isolectotype, WRSL!).

Small tree 1.5–3 m tall. Stems glabrous; immature stipules linear-lanceolate, connate at base, 6–12 mm long; mature ones not seen. Leaves with petiole 5–15 mm long, glabrous; blade elliptic, 8–15 by 2.5–5.5 cm, the apex acute to acuminate, the base acute, the surfaces pale green with yellow veins, glabrous. Inflorescences widely branching terminal panicles 7–15 cm long, bearing 15 to 50 flowers. Flowers with pedicel 1–3 mm long, densely puberulent; calyx rotate, split to near base into 4 reflexed, ovate lobes 1.5–3 mm long; corolla salverform with tube 8–12 mm long and 4 spreading, elliptic lobes 4–6 mm long that give upper portion of corolla distinctly 4-ribbed appearance before anthesis; stamens

4, epipetalous at top of tube, included, the anther linear-oblong, 2.5–3.5 mm long, subsessile; style shorter than tube, stigma lobes 1–1.5 mm long. Fruits oblong to pyriform, 10–16 mm long excluding persistent calyx, red at maturity, longitudinally ribbed when dry.

TYPIFICATION. Schumann listed two specimens, but these were probably destroyed at Berlin. However, there are duplicates of *Reinecke 242* (listed by Schumann as *241*) at G and US, and *Reinecke 635* at G and WRSL. I have designated *Reinecke 635* (G), collected from "Le Pua" (Lepue?), Upolu, as the lectotype.

DISTRIBUTION. Endemic to Upolu; foothill to montane forest, mostly in central portion of island; 350–500 m alt.

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** UPOLU: above Utumapu, *Rechinger 1570* (BM), *1686* (W); Mt. Vaea, *Reinecke 152, pro parte* (US), *242* (G, US); above Utumapu, *Whistler 1991* (BM, K, PTBG, US).

7. **Psychotria vaupelii** Whistler, sp. nov.

Psychotria chlorocalyx sensu Christoph. Bernice P. Bishop Mus. Bull. **154:** 50. 1938, *pro parte,* non Schumann.

Psychotria chlorocalyx affinis, a qua imprimis in foliis angustioribus, calyce et pedicello quasi glabris, et corolla longiore differt.

Shrub or small tree 1.5–4 m tall. Stems glabrous; stipules linear-lanceolate, connate at base, 6–12 mm long. Leaves with petiole 4–20 mm long, glabrous; blade narrowly elliptic to subfalcate, 7–16 by 1.5–3.5 cm (4–7 times longer than wide), the apex acuminate to attenuate, the base acute, the surfaces light green with yellow veins, glabrous. Inflorescences terminal, widely branching panicles 6–14 cm long, bearing 5 to 25 flowers. Flowers with pedicel 3–16 mm long, glabrous to puberulent; calyx rotate, split more than halfway into 4 ovate to triangular lobes 2–4 mm long, glabrous to puberulent on outside, subglabrous within; corolla salverform with tube 10–15 mm long and 4 elliptic lobes 7–10 mm long that give upper portion of corolla distinctly 4-ribbed appearance before anthesis, greenish; stamens 4, epipetalous in top of tube, partially exserted, the anther linear-oblong, 2.5–3.5 mm long, subsessile; style shorter than tube, stigma lobes 1–2 mm long. Fruits oblong to pyriform, 12–16 mm long excluding reflexed sepals, red at maturity, longitudinally ribbed when dry.

TYPE: Samoa, Savaii, above Ologogo, *Whistler 499* (holotype, PTBG!; isotype, BISH!).

DISTRIBUTION. Endemic to Savaii; understory tree in montane forest; 700–900 m alt.

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** SAVAII: above Matavanu, *Christophersen 2291* (A, BISH, K, US); above Salailua, *Christophersen 2906* (BISH); above Gagamalae, *Christophersen 3439* (BISH); *sine loco, Graeffe 1500* (HBG); Maugaloa, *Vaupel 635* (B, M); above Asau, *Whistler 1748* (K, PTBG).

This species is similar to *Psychotria chlorocalyx* but differs in having generally narrower leaves, nearly glabrous pedicels and calyces, and larger flowers. *Whistler 1748* appears to have infertile or diseased flowers.

Two other specimens should be mentioned here. *Whistler 1760* (B, BISH, K, PTBG) and *1761* (BISH, BM, PTBG, US), both collected above Asau, Savaii, appear to be hybrids intermediate between *P. vaupelii* and some other species, perhaps *P. savaiiensis*. Both of these possible parental species were collected on the same day in the same area (*Whistler 1745* and *1748*).

The species is named in honor of Dr. Friedrich Vaupel for his important botanical collections (which include a specimen of this species) made in Samoa from 1904 to 1906.

8a. **Psychotria carnea** (Forster f.) A. C. Smith subsp. **carnea,** Bernice P. Bishop Mus. Bull. **141:** 151. 1936; Christoph. Bernice P. Bishop Mus. Bull. **154:** 49. 1938; Yuncker, Bernice P. Bishop Mus. Bull. **220:** 255. 1959.

Petesia carnea Forster f. Fl. Ins. Austral. Prodr. 10. 1786. *Eumachia carnea* (Forster f.) DC. Prodr. **4:** 479. 1830. LECTOTYPE (here designated): Tonga, Namuka, *Forster 51* (BM!).

Chasalia pyriformis A. Gray, Proc. Amer. Acad. Arts **4:** 43. 1860. TYPE: Samoa, without further locality, 1839, *U. S. Expl. Exped. s.n.* (holotype, US?).

Small tree 2–5 m tall. Stems glabrous; young stipules linear and connate, mature ones not seen. Leaves with petiole 1.5–4.5 cm long, glabrous; blade obovate, 12–22 by 7–13 cm, apex acuminate, base acute to subattenuate, surfaces glabrous. Inflorescences broad, terminal panicles 3–8 cm long, bearing 15 to 30 flowers. Flowers with pedicel 3–10 mm long, glabrous; calyx campanulate to cup shaped, 3–5 mm long, shallowly divided into 4 broad lobes; corolla ca. 12–18 mm long (not seen mature), divided ca. halfway into 4 spreading to reflexed lobes that give upper portion distinct, 4-lobed appearance at anthesis, green, fleshy; stamens 4, epipetalous, included, the anther linear-oblong, 4–5 mm long, the filament ca. ½ as long as anther; style bifid at tip. Fruits obovate, 12–16 mm long (excluding calyx), red at maturity, finely longitudinally ribbed when dry, persistent cup-shaped calyx 5–7 mm wide.

TYPIFICATION. *Psychotria carnea* (*Petesia carnea*) is based on Forster's collection from Tonga in 1773. Two specimens of this are known to exist, an unnumbered one at K, and no. *51* collected from Namuka and stored at BM. I have designated the latter as lectotype. The type specimen of *Chasalia pyriformis,* collected by the U. S. Exploring Expedition, could not be located at GH or US and may be lost.

DISTRIBUTION. Indigenous to Samoa (Savaii), Tonga, and Fiji; understory shrub or small tree in foothill to montane forest; 250–450 m alt. (at least in Samoa).

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** SAVAII: above Gatavai, *Bristol 2294* (BISH, GH, US); above Sasina, *Cox 243* (BISH, GH); Ologogo, *Vaupel 385* (B, M, US); above Asau, *Whistler 17* (BISH, PTBG); above Palauli, *Whistler 1246* (B, BM, PTBG, US).

A sterile specimen, *Christophersen 3209* (BISH), collected above Sili, Savaii, probably also belongs to this species.

8b. **Psychotria carnea** subsp. **oncocarpa** (Schumann) Whistler, comb. nov.

Psychotria oncocarpa Schumann, Bot. Jahrb. Syst. **25:** 688. 1898; Rech. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **85:** 203. 1910. LECTOTYPE (here designated): Samoa, Upolu, Vailele?, *Reinecke 202* (G!).
Psychotria carnea sensu Christoph. Bernice P. Bishop Mus. Bull. **154:** 49. 1938, *pro parte*; sensu A. C. Smith, Bernice P. Bishop Mus. Bull. **141:** 151. 1936, *pro parte.*

Differs principally from subsp. *carnea* in having leaf blade elliptic, 8–16 by 4–8 cm, panicle 5–12 cm long, calyx 2–3.5 mm long, style as long as tube, stigma lobes 1–2 mm long, and fruits 10–15 mm long, orange at maturity, with persistent calyx 3–5 mm wide.

TYPIFICATION. In his description of *Psychotria oncocarpa,* Schumann did not list any specimens, only the collection locality of Vailele, Upolu. Two Reinecke specimens without locality (*202* and *349,* both at G) have been found. I have designated *Reinecke 202* (G) as the lectotype.

DISTRIBUTION. Endemic to Upolu and possibly Savaii;[3] understory tree in foothill to montane forest, 250–600 m alt.

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** SAVAII: *sine loco, Graeffe 144, pro parte* (HBG), *216, pro parte* (HBG). UPOLU: Moamoa, *Eames 202* (BISH, GH, K, US); *sine loco, Graeffe 7a* (HBG), *18c* (HBG); Mt. Vaea, *Rechinger 1196* (BM, K), *1738* (W); above Utumapu, *Rechinger 1690* (BM, US, W); Vailele(?), *Reinecke 349* (G); Mt. Mariota, *Whistler 817* (PTBG, US); Afulilo, *Whistler 1567* (BISH, K, PTBG). WITHOUT FURTHER LOCALITY: *Powell 345* (K).

9. **Psychotria bristolii** Whistler, sp. nov. FIGURE 1.

Arbor 6–12 m alta. Folia elliptica, 14–26 cm longa et 2–8 cm lata; petiolus 4–8.5 cm longus. Inflorescentia multiflora, axillaris, 15–25 cm longa; pedunculus crassus. Calyx cupulatus, 3–5 mm longus. Corolla salverformis, tubo 3–4 cm longo, lobis 5, 12–18 mm longis. Fructus ellipsoideus, compressus, 20–33 mm longus, 2-costatus; calyx persistens.

Small to medium-sized tree 6–12 m tall. Stems glabrous; stipules connate their entire length to form cup-shaped to cylindrical sheath with truncate to rounded apex, 3.5–5 cm long. Leaves with petiole 4–8.5 cm long, glabrous; blade elliptic, 14–26 by 4–8 cm, apex acute to mucronate, base acute, surfaces glabrous. Inflorescences many-flowered, branching panicles 15–25 cm long on stout peduncle in upper axil. Flowers with pedicel 1–2 cm long, glabrous; calyx cup shaped, 3–5 mm long, margin entire or finely serrate; corolla salverform with tube 3–4 cm long and 5 spreading, linear-lanceolate lobes 12–18 mm long, white, glabrous inside and out; stamens 5, epipetalous in upper throat, partially exserted, the anther linear-oblong, 4–6 mm long, the filament ca. 1 mm long; style 3.5–4.5 cm long, slightly exserted, stigma lobes 2–3 mm long. Fruits

[3]Since the only record of this subspecies from Savaii is based on Graeffe's specimens, the data for which are sometimes erroneous, the species may actually be restricted to Upolu. Additionally, both of these Graeffe specimens are mixed.

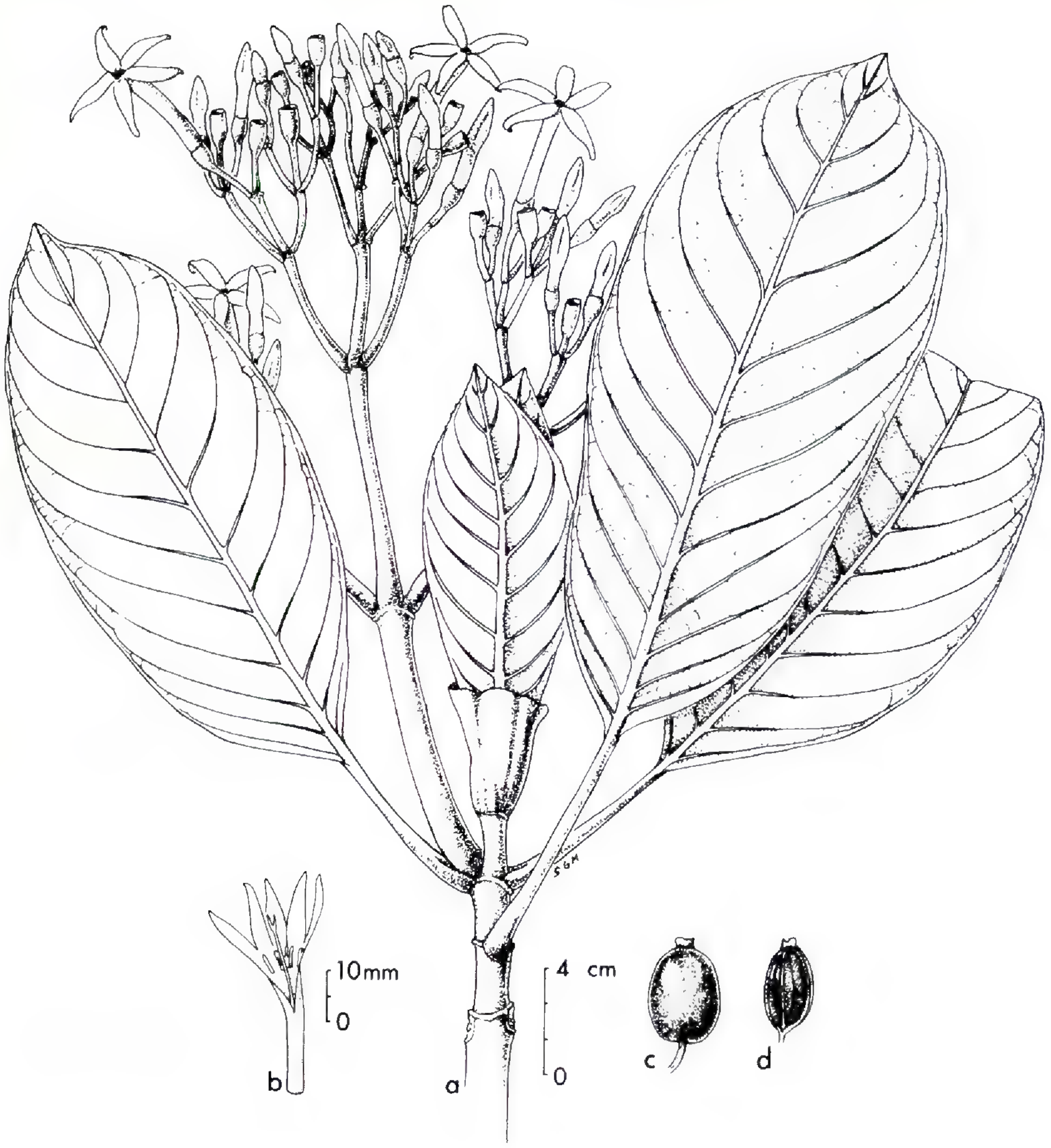

FIGURE 1. **Psychotria bristolii:** a, flowering stem; b, flower; c, fresh fruit; d, dry fruit.

ellipsoid, 20–33 mm long, laterally compressed with single prominent transverse rib on each pyrene face, crowned by persistent calyx.

TYPE: Samoa, Savaii, above Aopo, *Bristol 2162* (holotype, BISH!; isotypes, GH!, K!).

DISTRIBUTION. Endemic to Savaii; understory tree in montane to cloud forest; 900 m alt. Only three specimens are known, all collected on the north-central slopes of Savaii.

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** SAVAII: above Matavanu, *Christophersen 2038* (BISH); above Asau, *Whistler 1754* (B, K, PTBG).

This species differs from any other *Psychotria* in Samoa, most strikingly by its large, ellipsoid fruit with a single transverse rib on each pyrene face, and

by its stout, axillary inflorescence with large, showy, white flowers. Of the other Samoan *Psychotria* species, only *P. grandistipulata* has flowers as large as these. *Psychotria bristolii* does not appear to have any close relatives in Samoa. It was first collected by Christophersen but was not mentioned in any of his publications. Both his specimen and the one collected by Bristol are in fruit, while *Whistler 1754* is in flower.

Psychotria bristolii is named in honor of Mel Bristol, who made an excellent collection of plants, including a specimen of this species, in Samoa in 1968.

10. **Psychotria grandistipulata** (Lauterbach) Whistler, comb. nov. FIGURE 2.

Randia grandistipulata Laut. Bot. Jahrb. Syst. **41:** 236. 1908; Rech. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **85:** 194. 1910. TYPE: Samoa, Savaii, above Aopo, *Vaupel 388* (holotype, WRSL!; isotypes, B!, BISH!, K!).

Small to medium-sized tree up to 10 m tall. Stems distinctly marked by annular stipule scars and leaf scars; stipules obovate, with rounded tip often recurved, connate entire length to form persistent, cup-shaped involucre (enclosing stem tip, young leaves, and base of inflorescence) 2–3 by 2.5–3.5 cm, whitish green, glabrous, often more than 1 present at a time. Leaves with petiole 1.5–5 cm long, glabrous; blade elliptic to oblanceolate, 8–24 by 2.5–7.5 cm, apex acute to acuminate, base acute, surfaces glabrous. Inflorescences panicles 3–10 cm long, arising in upper axil, with 3 to 10 flowers. Flowers with pedicel 3–20 mm long, with paired deciduous bracteoles up to 5 mm long at proximal end; calyx narrowly campanulate to urceolate, 10–15 mm long, shallowly 5-lobed, glabrous; corolla salverform with narrow tube 2–4.5 cm long and 5 linear-lanceolate, recurved lobes 2–3.5 cm long; stamens 5, epipetalous at top of throat, the anther linear-oblong, 4–6 mm long, subsessile; style shorter than tube, stigma lobes 2–4 mm long. Fruits ovoid to urceolate, 2.5–4.2 cm long including cylindrical, persistent calyx, dark purple at maturity, with single prominent transverse rib on each pyrene face when dry.

TYPIFICATION. *Psychotria grandistipulata* is based on *Vaupel 388,* collected in 1906 above Aopo. Lauterbach named this a *Randia,* but because there are only two ovules in the fruit, the species has to be a *Psychotria* instead. Rechinger followed Lauterbach without comment, and Christophersen, who collected it six times, labeled his specimens "*Randia*?" but for some reason did not mention them in his publications. Duplicates of *Vaupel 388* exist at B, BISH, K, and WRSL. I consider the sheet of *Vaupel 388* at WRSL to be the holotype.

DISTRIBUTION. Endemic to Savaii and Upolu; understory tree in montane forest; 500–1000 m alt.

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** SAVAII: above Aopo, *Bristol 2150* (BISH, GH, K, PTBG, US); E of Olo, *Christophersen 2313* (BISH, K, US); Olo, *Christophersen 2514* (BISH, K, US); above Salilua, *Christophersen 2690* (BISH, K, US), *2944* (BISH, K, US); Siuvao-Auala, *Christophersen 3376* (BISH, K); Maugaafi, *Rechinger 64* (W), *1586* (W); above Ologogo, *Whistler 536* (BM, K, PTBG, US). UPOLU: above Malololelei, *Christophersen 233* (BISH); above Tapatapao, *Cox 128* (BISH, GH); Lanoanea, *Cox 149* (BISH, GH, K); Tiavi Pass, *Cox 178* (BISH, GH, K); Tiavi, *Whistler 1068* (B, K, PTBG, US), *2462* (BISH, K, PTBG); Lanoanea, *Whistler 1083* (PTBG); Lepue, *Whistler 4143* (B, BISH, PTBG, US).

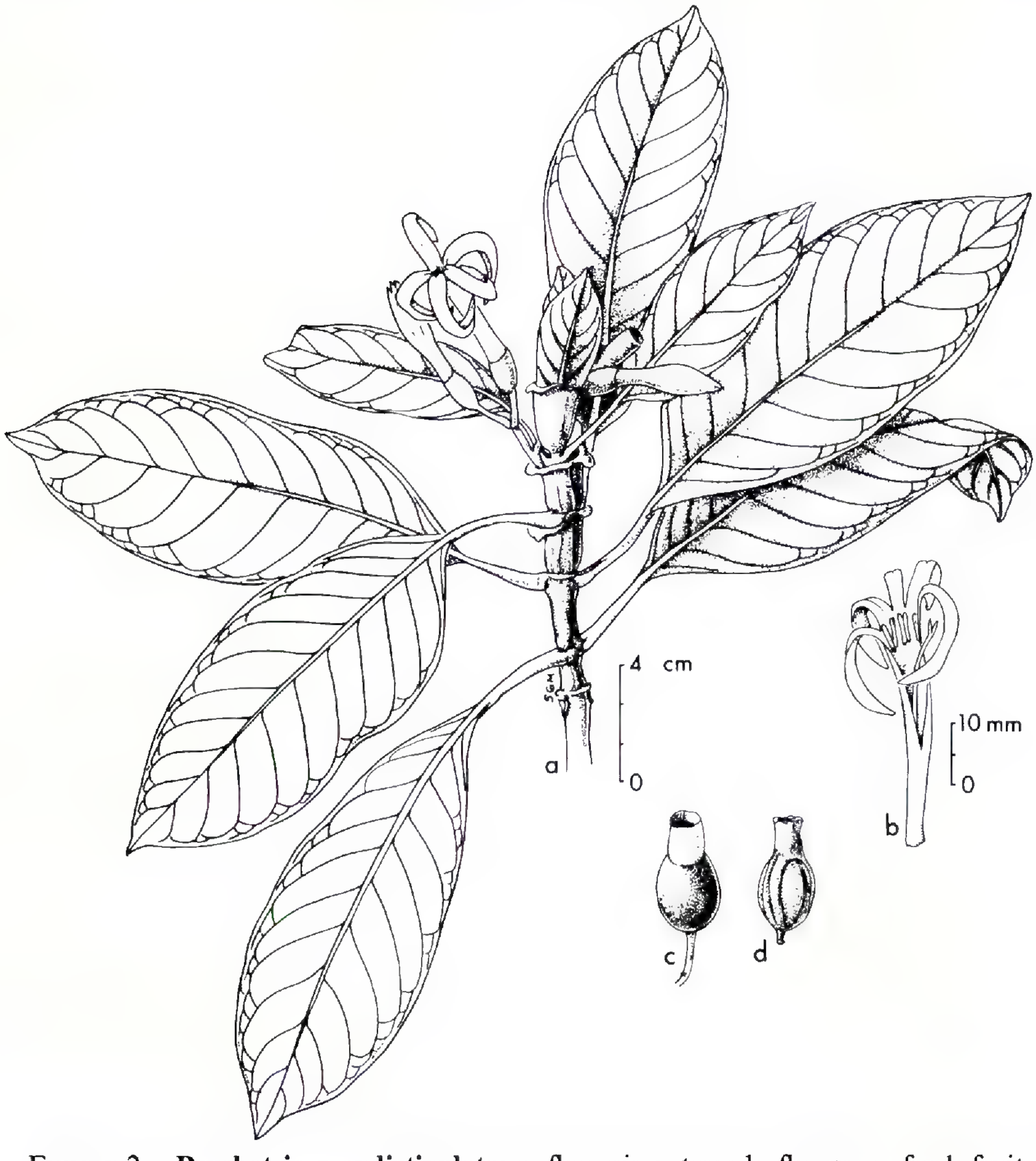

FIGURE 2. **Psychotria grandistipulata:** a, flowering stem; b, flower; c, fresh fruit; d, dry fruit.

This species differs most notably from any other in Samoa by its connate, whitish green stipules that form a cup-shaped involucre with the tip often recurved, and by its often-purplish fruits. Also, it has the largest flowers of any species of *Psychotria* in Samoa.

11. **Psychotria juddii** Christoph. Bernice P. Bishop Mus. Bull. **154:** 56. 1938.

TYPE: Samoa, Savaii, forest above Gagamalae, above 900 m, 1931, *Christophersen 3424* (holotype, BISH!; isotypes, A!, K!).

Small tree up to 6 m tall. Stems glabrous, leaves concentrated at ends of branches; stipules lanceolate, split at tip into 2 short lobes, connate over half their length, 15–30 mm long. Leaves with petiole 2–6 cm long, glabrous; blade oblong to elliptic or slightly obovate, 14–32 by 5.5–11 cm, apex acute to

acuminate, base acute or short-attenuate, surfaces glabrous. Inflorescences solitary erect globose heads 2.5–3 cm across, bearing up to 45 flowers, the peduncle 2–4.5 cm long, covered with reddish brown hairs. Flowers with calyx cup shaped, shallowly divided into 5 obtuse lobes, glabrous; corolla infundibular with tube 35–45 mm long and 5 fleshy, recurved linear lobes up to 2 cm long, white, scurfy-pubescent on outside, densely pubescent within; stamens 5, epipetalous in middle of throat, the anther linear-oblong, 2–3 mm long, the filament 6–7 mm long; style as long as tube, stigma lobes up to 5 mm long. Fruits globose, ca. 3.5 cm in diameter including persistent fleshy calyx, red at maturity, not obviously longitudinally ribbed when dry.

DISTRIBUTION. Endemic to Savaii; understory tree in cloud forest; above 900 m alt.

ADDITIONAL SPECIMEN EXAMINED. **Samoa.** SAVAII: above Salailua, *Christophersen 2706* (BISH).

This rare species has been collected only twice, both times by Christophersen. With its capitate inflorescences, it does not appear to be closely related to any other Samoan species of *Psychotria*.

12. **Psychotria gigantopus** Schumann, Bot. Jahrb. Syst. **25:** 686. 1898; Christoph. Bernice P. Bishop Mus. Bull. **154:** 53. 1938. NEOTYPE (here designated): Samoa, without further locality, *Reinecke 459* (WRSL (fragment)).

Small tree up to 5 m tall. Stems 6–10 mm thick, glabrous, with leaves clustered at ends; stipules not seen. Leaves appearing nearly whorled; petiole 3–16 mm long, glabrous; blade oblanceolate, 18–45 by 5–11 cm, apex acuminate, base cuneate to rounded, surfaces glabrous. Inflorescences drooping, terminal panicles 20–40 cm long, bearing subumbellate clusters of 12 to 24 flowers on whorled branches congested on upper half of peduncle. Flowers with pedicel 1–10 mm long, glabrous; calyx campanulate to cylindrical, 5–9 mm long, shallowly divided into 5 lobes less than 1 mm long, glabrous; mature corolla unknown, probably tubular, white, 5-lobed; stamens 5, epipetalous, the anther oblong, 2–3 mm long, the filament short; mature style unknown. Fruits oblong to obovoid, 2.5–3.5 cm long excluding persistent calyx, red at maturity, shallowly longitudinally ridged when dry.

TYPIFICATION. *Psychotria gigantopus* was based on *Reinecke 633,* collected at "Lona Fai" on Upolu in 1895. Christophersen (1938) noted seeing this specimen at B (now destroyed), as well as another one, *Reinecke 459.* The latter one was not mentioned by Schumann, and in fact the number is ascribed by Reinecke to a specimen belonging to an entirely different family. A fragment of it (indeed this species) is located at WRSL, and I have designated this specimen to be the neotype.

DISTRIBUTION. Endemic to Samoa; understory tree in cloud forest of Upolu and Savaii; 700–1200 m alt.

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** SAVAII: Mauga Mu, *Baker s.n.* (PTBG); above Matavanu, *Christophersen 834* (A, BISH), *2125* (BISH, K), *2194* (A, BISH, K); Maugaloa, *Vaupel 402* (B, M). UPOLU: above Falemauga, *Cox 30* (BISH, GH). WITHOUT FURTHER LOCALITY: *Whitmee 138* (MEL).

This species differs from any other in Samoa in having large panicles with subumbellate clusters of flowers, and large, oblanceolate leaves appearing to be whorled at the ends of the branches.

13. **Psychotria closterocarpa** A. Gray, Proc. Amer. Acad. Arts **4:** 44. 1860; Christoph. Bernice P. Bishop Mus. Bull. **154:** 50. 1938. TYPE: Samoa, without further locality, 1839, *U. S. Expl. Exped. s.n.* (holotype, US *62348*!; isotype, GH!).

Psychotria dolichocarpa Schumann, Bot. Jahrb. Syst. **25:** 686. 1898; Rech. Denkschr. Kaiserl. Acad. Wiss., Math.-Naturwiss. Kl. **85:** 200. 1910. LECTOTYPE (here designated): Samoa, Upolu, Lonafai and Lepua [Lepue?], 1895, *Reinecke 634* (G!).

Small tree 3–6 m tall. Stems glabrous; stipules obovate, connate for over half their length, up to 3 cm long. Leaves with petiole 5–9 cm long, glabrous; blade elliptic to obovate, 20–35 by 4–13 cm, apex acuminate to nearly rounded, base acute, surfaces glabrous. Inflorescences terminal panicles 10–20 cm long, often branching near base, bearing 40 to 150 flowers. Flowers with pedicel 1–7 mm long, glabrous; calyx campanulate, 3.5–5.5 mm long, entire to shallowly 5-lobed; corolla tubular with tube 20–25 mm long and 5 (rarely 6) lanceolate spreading lobes 4.5–6.5 mm long, white; stamens 5 (rarely 6), epipetalous in upper throat, partially exserted, the anther linear-oblong, 2–3.5 mm long, the filament ca. ½ as long as anther; style shorter than tube, stigma lobes 4–6 mm long. Fruits ellipsoid, 15–20 mm long excluding persistent calyx, orange at maturity, longitudinally ribbed when dry. $n = 22$ (*Whistler 1643*).

DISTRIBUTION. Endemic to Savaii and Upolu; understory tree in montane to cloud forest; 550–1200 m alt.

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** SAVAII: above Aopo, *Bristol 2148* (BISH, GH, K); above Gataivai, *Bristol 2277* (BISH); above Patamea, *Bristol 2325* (BISH); above Salailua, *Christophersen 2917* (BISH, K), *3068* (BISH, US); above Gagamalae, *Christophersen 3440* (BISH); above Sasina, *Cox 257* (BISH, GH, K); *sine loco, Graeffe 119* (HBG); above Ologogo, *Whistler 544* (B, BM, PTBG, US). UPOLU: near Malololelei, *Christophersen 312* (BISH); above Saluafata, *Christophersen 524* (A, BISH, M); Tapatapao, *Cox 138* (BISH, GH, K), *392* (GH); *sine loco, Graeffe 40* (W); *sine loco, Kramer s.n.* (WRSL (fragment)); near Tiavi, *Rechinger 439* (W), *454* (W); Lanotoo, *Rechinger 457* (W), *1808* (W), *1846* (W); Afiamalu, *Whistler 804* (B, BISH, PTBG, US); Lanoataata, *Whistler 1504* (BISH, PTBG, US); near Tiavi, *Whistler 1643* (B, BISH, K, PTBG, US); SE of Mt. Mariota, *Whistler 1895* (BISH, PTBG). WITHOUT FURTHER LOCALITY: *Reinecke s.n.* (WRSL).

14. **Psychotria pacifica** Schumann, Bot. Jahrb. Syst. **25:** 687. 1898; Rech. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **85:** 200. 1910; Christoph. Bernice P. Bishop Mus. Bull. **154:** 57. 1938. TYPE: Samoa, Upolu, above Vailele, *Reinecke 318* (lectotype, here designated, G!; isolectotypes, K!, US!, WRSL!).

Psychotria stenocarpa Schumann, Bot. Jahrb. Syst. **25:** 687. 1898. Christoph. Bernice P. Bishop Mus. Bull. **154:** 58. 1938. Var. *typica* Hochr. Candollea **5:** 269. 1934. TYPE: Samoa, Savaii, mountain region, 1894, *Reinecke 348* (B, presumably destroyed).

Psychotria stenocarpa subsp. *montivaga* Rech. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **85:** 201. 1910. TYPE: Samoa, Savaii, in deep forest on Mt. Maugaafi, ca. 1200 m alt., 1905, *Rechinger 412* (holotype, W).

Psychotria loniceroides Rech. Feddes Repert. Spec. Nov. Regni Veg. **6:** 328. 1909; Rech. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **85:** 200. 1910. TYPE: Samoa, near Maugaafi, ca. 1500 m alt., 1905, *Rechinger 1075* (holotype, W).

Psychotria upoluensis Christoph. Bernice P. Bishop Mus. Bull. **154:** 61. 1938. TYPE: Samoa, Upolu, forest on Maugatele ridge above Saluafata, 600 m alt., 1929, *Christophersen 532* (holotype, BISH).

Shrub or small tree 1–6 m tall. Young stems, petioles, and peduncles glabrous or sparsely covered with short, erect, reddish brown hairs; stipules lanceolate with 2 acute lobes, connate for about half their length, 10–18 mm long. Leaves with petiole 1–5 cm long; blade lanceolate to oblanceolate, 8–20 by 1.8–6 cm (2.5–5 times longer than wide), the apex acuminate, the base acute, the surfaces glabrous, sometimes reddish and mottled when dried (usually those specimens with reddish brown hairs). Inflorescences terminal panicles 1–5 cm long with 1 to 5 simple or branched peduncles bearing up to 80 subsessile flowers in dense, compact umbels. Flowers with calyx campanulate, 2.5–3.5 mm long, shallowly divided into 5 rounded to triangular lobes; corolla tubular with tube 15–25 mm long and 5 lobes 5–8 mm long, white, usually glabrous on outside, densely pilose to subglabrous within; stamens 5, epipetalous in upper throat, included to slightly exserted, the anther linear-oblong, 2–3 mm long, the filament less than ½ as long as anther; style about as long as corolla, exserted, stigma lobes 1–2 mm long. Fruits ovoid, 10–15 mm long excluding persistent calyx, red to orange at maturity, longitudinally ribbed when dry.

TYPIFICATION. Schumann cited three specimens in his description of the species. Duplicates exist for all three, and I have designated *Reinecke 318* (G), collected in 1894 above Vailele, Upolu, as the lectotype. Isolectotypes of this are at K, US, and WRSL.

DISTRIBUTION. Probably endemic to Savaii and Upolu;[4] understory tree in foothill to cloud forest; 350–1500 m alt.

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** SAVAII: above Aopo, *Bristol 2149* (BISH, GH, K); above Salailua, *Bryan 171* (BISH); above Letui, *Christophersen 737* (BISH), *740* (BISH); near Mataulano Lake, *Christophersen 877* (BISH); above Matavanu, *Christophersen 1985* (A, BISH); NE of Salailua, *Christophersen 2569* (A, BISH, K, US, W); above Salailua, *Christophersen 2694* (A, BISH), *2739* (BISH, K, US); above Sasina, *Cox 241* (BISH, GH), *259* (BISH, GH); *sine loco, Graeffe 137* (HBG); Maugaafi, *Rechinger 412* (W); near Maugaafi, *Rechinger 1075* (W); near Aopo, *Rechinger 1603* (W); *sine loco, Vaupel 73* (B); Maugaloa, *Vaupel 450* (B, BISH, K, US), *488* (B, M, US); Sologa, *Vaupel 638* (M); above Ologogo, *Whistler 517* (B, BISH, PTBG, US); above Asau, *Whistler 1763* (B, BISH, BM, K, PTBG, US). UPOLU:

[4]One specimen collected by Graeffe over a century ago was labeled as being from Tutuila, but since many of Graeffe's localities have proved to be erroneous and the species has not been collected on that island again, it is doubtful if it ever occurred there.

Malololelei–Lanotoo trail, *Christophersen 395* (BISH); above Eva, *Christophersen 527* (A, BISH, K); Maugatele Ridge, *Christophersen 532* (BISH), *540* (A, BISH, K); Lanoanea, *Cox 150* (GH); Lepue, *Cox 203* (GH); *sine loco, Graeffe 15* (W), *17ii* (HBG), *112* (BM), *1368* (HBG, K), *s.n.* (K); Lanotoo, *Hochreutiner 3241* (G); near Tiavi, *Rechinger 400* (BM, K, US, W), *444* (W), *462* (BM, W), *1315* (W); near Lanotoo, *Rechinger 1849* (W); near Lanotoo, *Reinecke 320* (G); Tofua, *Reinecke 320a* (G); Mt. Fito–Lepue, *Sledge s.n.* (K); near Lanotoo, *Whistler 271* (PTBG); Mt. Sigaele, *Whistler 352* (B, BISH, PTBG, US); near Lemafa Pass, *Whistler 438* (BISH, PTBG); near Utumapu, *Whistler 686* (B, BISH, PTBG, US); near Lepue, *Whistler 737* (B, BISH, PTBG, US); rim of Mt. Fiamoe, *Whistler 1162* (PTBG); below Lanoataata, *Whistler 1487* (B, BISH, K, PTBG, US); near Tiavi, *Whistler 1644* (B, BISH, K, PTBG, US); SE of Mt. Mariota, *Whistler 1921* (PTBG); rim of Mt. Fiamoe, *Whistler 2006* (BISH, PTBG); rim of Mt. Taitoelau, *Whistler 2055* (PTBG); S of Mt. Fito, *Whistler 3979* (BISH, PTBG); above Apia, *Wilder 418a* (BISH), *418b* (BISH). TUTUILA: *sine loco, Graeffe 1383* (HBG, K). WITHOUT FURTHER LOCALITY: *Whitmee 81* (K, MEL (mix)), *101* (BM, K, MEL), *129* (K).

Schumann named *Psychotria pacifica* based on three specimens, and *P. stenocarpa* based on one. This last specimen, *Reinecke 348,* collected in the mountain region of Savaii, has been lost, but on the basis of Schumann's descriptions, the differences between the two species do not seem to be significant. Christophersen, who described *P. upoluense,* noted only that his species differed in having the corolla pubescent on the outside, but this difference is well within the range of variation of *P. pacifica. Psychotria loniceroides* and *P. stenocarpa* subsp. *montivaga,* both described by Rechinger, also appear to differ little from *P. pacifica.* The species is quite variable in foliage and pubescence, but the panicle of subumbellate clusters is distinctive. One specimen that is particularly anomalous, however, is *Vaupel 488.* It is more densely red-hairy than any other specimens seen, and its leaves are up to 9 cm wide (vs. less than 6 cm in other specimens). However, because of the variability of this species, it seems unwise at this time to deal with this single specimen other than to mention it.

15. **Psychotria apodantha** A. Gray, Proc. Amer. Acad. Arts **4:** 46. 1860; Christoph. Bernice P. Bishop Mus. Bull. **154:** 48. 1938. TYPE: Samoa, without further locality, 1839, *U. S. Expl. Exped. s.n.* (holotype, US *67258*!; isotype, GH (fragment)!).

Psychotria angustissima Rech. Feddes Repert. Spec. Nov. Regni Veg. **6:** 327. 1909; Rech. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **85:** 201. 1910. TYPE: Samoa, Savaii, forest near Patamea, 1905, *Rechinger 1141* (holotype, W!).

Shrub or small tree 1–2 m tall. Young stems densely covered with erect, reddish brown hairs; stipules divided into 2 linear to lanceolate lobes, connate for most of their length, up to 2 cm long, margin usually densely hairy. Leaves with petiole 0.8–2 cm long, sparsely to densely covered with erect reddish brown hairs up to 2 mm long; blade lanceolate, 8–17 by 0.8–3 cm (5–10 times longer than wide), apex attenuate, base acute, upper surface subglabrous to sparsely appressed-hairy, lower surface glabrous or with few scattered hairs on basal midvein. Inflorescences terminal solitary umbels bearing up to 10 subsessile flowers. Flowers with calyx campanulate, 4.5–6 mm long, shallowly

divided into 5 triangular lobes up to 1 mm long, subglabrous to hirsute; corolla tubular with tube 18–23 mm long and 5 spreading lobes 6–9 mm long, white, subglabrous on outside, densely pilose within; stamens 5, epipetalous in upper throat, the anther linear, 2–3 mm long, filament less than ½ as long as anther; style up to 24 mm long, included, stigma lobes ca. 2–3.5 mm long. Fruits obovoid, 8–12 mm long excluding persistent calyx, red at maturity, pubescent when young, longitudinally ribbed when dry.

DISTRIBUTION. Endemic to Savaii and Upolu; understory shrub in coastal to lowland forest near coast, mostly on old lava flows below 75 m elevation. The single specimen collected on Upolu, however, was from montane forest on an old cinder cone at 650 m alt.; one from Savaii (*Christophersen 2751*) was collected at 1200–1300 m.

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** SAVAII: Salailua, *Bryan 168* (BISH); Lealatele, *Christophersen 2472* (A, BISH, US); above Salailua, *Christophersen 2751* (BISH); Salailua-Lataiuta, *Christophersen 2872* (BISH, K); Sili-Lataiuta, *Christophersen 3138* (BISH); Faala-Tafuatai, *Cox 107* (BISH, GH, K); *sine loco, Reinecke s.n.* (WRSL (fragment)); Tafuauta, *Whistler 1222* (B, BISH, PTBG, US). UPOLU: SE of Mt. Mariota, *Whistler 1905* (B, BISH, K, PTBG). WITHOUT FURTHER LOCALITY: *Whitmee 57* (K), *s.n.* (BM).

Psychotria apodantha is most closely related to *P. pacifica,* from which it most obviously differs in having narrower leaves and sessile, unbranched inflorescences. *Reinecke 420,* collected on Savaii without further locality, could not be found and is probably lost.

16. **Psychotria reineckei** Schumann, Bot. Jahrb. Syst. **25:** 686. 1898; Rech. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **85:** 199. 1910; Christoph. Bernice P. Bishop Mus. Bull. **154:** 58. 1938. TYPE: Samoa, Savaii, central mountains, 1894, *Reinecke 423* (lectotype, here designated, BISH!; isolectotypes, BM!, G!, WRSL!).

Psychotria elegantula Rech. Feddes Repert. Spec. Nov. Regni Veg. **7:** 168. 1909; Rech. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **85:** 199. 1910; Hochr. Candollea **5:** 269. 1934. TYPE: Samoa, Upolu, forest near Lanotoo, ca. 700 m alt., 1905, *Rechinger 151* (holotype, W!).

Small tree 2–4 m tall. Stems glabrous; stipules obovate with 2 acute to mucronate lobes, connate for over half their length to form campanulate sheath, 2–5 cm long. Leaves with petiole 1–5 cm long, glabrous; blade lanceolate to oblanceolate, 6–26 by 2.5–6.5 cm, the apex acuminate, the base acute, the surfaces glabrous, drying reddish brown or mottled. Inflorescences terminal, many-flowered panicles 3–7 cm long, with 1 to 3 branches at base. Flowers with pedicel 3–12 mm long, glabrous; calyx cylindrical, 6–9 mm long, divided about halfway into (4 or) 5 (or 6) oblong lobes, white, not persisting on fruit; corolla tubular with tube 11–16 mm long and 5 linear-oblong lobes 7–10 mm long, white; stamens (4 or) 5 (or 6), epipetalous in upper throat, mostly included, the anther oblong, 3–4 mm long, filament 3–5 mm long; style about as long as tube, stigma lobes 2.5–4 mm long. Fruits ovoid, 10–14 mm long, pink to flesh colored at maturity, shallowly 3- or 4-ribbed on each pyrene face when dry.

TYPIFICATION. *Psychotria reineckei* was based on *Reinecke 423,* collected in the central mountain region of Savaii in 1894. The holotype at B was presumably destroyed, but there are duplicates at BISH, BM, G, and WRSL. *Reinecke 423* at BISH is hereby designated as the lectotype.

DISTRIBUTION. Endemic to Savaii and Upolu; understory tree in montane to cloud forest; 600–1700 m alt.

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** SAVAII: above Aopo, *Bristol 2126* (BISH, GH, K); *sine loco, Vaupel 80* (B); Maugaloa, *Vaupel 636* (B, M, PTBG); S of Mataana, *Vaupel 669* (B). UPOLU: above Malololelei, *Christophersen 258* (A, BISH), *265* (BISH, K, US); above Saluafata, *Christophersen 531* (BISH); Lanotoo, *Hochreutiner 3262* (G); Lanotoo, *Rechinger 737* (W), *764* (W), *1907* (W), *1916* (W), *1958* (BM, W); Mt. Fito, *Whistler 3964* (B, BISH, PTBG, US); Lepue, *Whistler 4151* (BISH, PTBG, US). WITHOUT FURTHER LOCALITY: *Powell 246* (K).

This species is distinctive with its white, oblong-lobed calyx and its large, campanulate stipule sheath.

17. **Psychotria garberiana** Christoph. Bernice P. Bishop Mus. Bull. **154:** 51. 1938; Yuncker, Bernice P. Bishop Mus. Bull. **184:** 65. 1945. TYPE: Samoa, Olosega, Olosegauta-Piumafua ridge, 500 m alt., 1925, *Garber 1062* (holotype, BISH!).

Small tree 2–4 m tall. Stems glabrous; stipules elliptic with notched tip, connate over half their length, 6–16 mm long. Leaves with petiole 3–25 mm long, glabrous; blade elliptic to oblanceolate, 5–16 by 1.5–7 cm, the apex acute to subacuminate, the base acute to subattenuate, the surfaces glabrous, often drying to mottled reddish brown. Inflorescences terminal or upper-axillary panicles 3–6 cm long and nearly as wide, bearing 6 to 30 flowers, often branched at base. Flowers with pedicel 3–8 mm long, glabrous; calyx campanulate, 2.5–5 mm long, shallowly divided ca. 1 mm into 5 triangular lobes, glabrous; corolla tubular with narrow tube 13–20 mm long and 5 lanceolate lobes 4–8 mm long, white, glabrous on outside, villous within; stamens 5, epipetalous in upper throat, included, the anther oblong, 2–3 mm long, the filament ½ to nearly as long; style shorter than tube, stigma lobes 2–3 mm long. Fruits ovoid to subglobose, 8–12 mm long excluding persistent, cup-shaped calyx, orange to pink at maturity, longitudinally ribbed when dry.

DISTRIBUTION. Endemic to Manua (Ofu, Olosega, and Tau); understory tree in foothill to montane forest; 300–800 m alt.

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** OFU: summit of island, *Whistler 3030* (K, PTBG). OLOSEGA: Piumafua, *Whistler 3078* (K, PTBG). TAU: summit, *Garber 754* (BISH); above Luma, *Whistler 1412* (B, BISH, G, PTBG, US); above Fitiuta, *Whistler 3134* (PTBG); near summit, *Whistler 3197* (B, K, PTBG). WITHOUT FURTHER LOCALITY: *Powell 280* (K).

18. **Psychotria christophersenii** Whistler, sp. nov. FIGURE 3.

Psychotria aff. *reineckei* sensu Christoph. Bernice P. Bishop Mus. Bull. **154:** 58. 1938.

Ad Psychotria garberianam affinis, a qua imprimis differt stipulis non fissis, corolla longiore, et fructu curvato longiore.

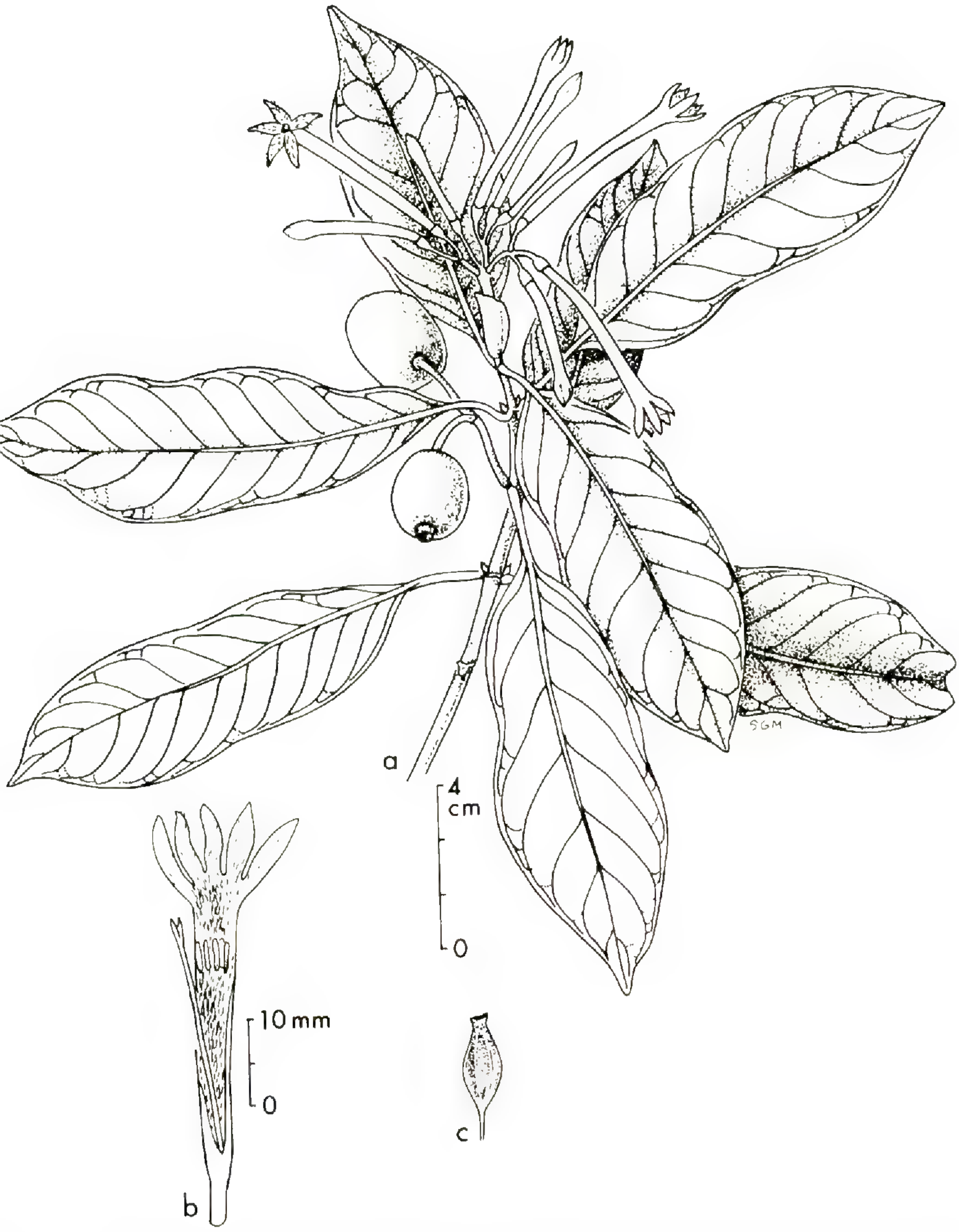

FIGURE 3. **Psychotria christophersenii:** a, flowering and fruiting branch; b, flower; c, dry fruit.

Shrub or small tree up to 5 m tall. Stems glabrous; stipules obovate with apex obtuse to rounded, connate for over half their length, 15–25 mm long. Leaves with petiole 1–2 cm long, glabrous; blade usually oblanceolate, 6–12 by 1.5–4.5 cm, the apex short-acute, the base acute, the surfaces glabrous, often drying mottled reddish brown. Inflorescences terminal or upper-axillary panicles 2–5 cm long, divided at base into 3 branches, each bearing 3 to 10 flowers. Flowers with pedicel 1–7 mm long, glabrous; calyx campanulate, 2–4 mm long, shallowly divided into 5 lobes up to 1 mm long, glabrous; corolla tubular with narrow tube 22–45 mm long and 5 lanceolate lobes 5–9 mm long, white, glabrous on outside, villous within; stamens 5, epipetalous in upper throat,

included, the anther linear-oblong, 3–4.5 mm long, the filament up to ½ as long; style shorter than tube, stigma lobes 2–4 mm long. Fruits narrowly ovoid and often somewhat curved, 12–18 mm long excluding persistent, cup-shaped calyx, pink at maturity, longitudinally ribbed when dry.

TYPE: Samoa, Savaii, S of Mt. Silisili, *Whistler 2666* (holotype, PTBG!; isotypes, B!, BISH!, K!).

DISTRIBUTION. Endemic to Savaii; understory tree in cloud forest; 1300–1700 m alt.

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** SAVAII: above Letui, *Christophersen 774* (BISH); above Matavanu, *Christophersen 2272* (A, BISH); Safotu-Salailua, *Christophersen 2559* (BISH); Maugaafi, *Rechinger 634* (W), *1950* (W); central mountain region, *Vaupel 294* (B, K, M, WRSL (fragment)); W of Mt. Silisili, *Whistler 2521* (B, BISH, K, PTBG), *2666A* (PTBG); SW of Mt. Silisili, *Whistler 2657* (PTBG).

Psychotria christophersenii is most closely related to *P. garberiana* but differs in having longer, elliptic to subcylindrical (vs. globose to subglobose) fruits, longer flowers, and longer, unnotched stipules. The fruit and calyx are very similar to those of *P. closterocarpa,* but otherwise the two species are quite different. Outside Samoa, *P. christophersenii* appears to be related to *P. grantii* Fosberg, of Tahiti, and *P. temehaniensis* J. W. Moore, of Raiatea.

Psychotria christophersenii was first collected by Vaupel in 1906 but was incorrectly identified as *P. reineckei.* Christophersen, who collected it three or four times, was the first to recognize that a distinct species was involved, but since his specimens lacked flowers, he merely listed it as *P.* aff. *reineckei. Christophersen 2143* (BISH), collected above Matavanu, Savaii, probably also belongs here, but its calyx is reminiscent of *P. xanthochlora.*

This species is named in honor of Erling Christophersen, whose work in Samoan botany is unequaled to this time.

19. **Psychotria xanthochlora** Schumann, Bot. Jahrb. Syst. **25:** 687. 1898; Rech. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **85:** 200. 1910; Christoph. Bernice P. Bishop Mus. Bull. **154:** 62. 1938. TYPE: Samoa, Upolu, above Saluafata, *Christophersen 526* (neotype, here designated, BISH!; isoneotypes, K!, US!).

Small tree 2–4 m tall. Stems glabrous; stipules ovate to elliptic with notched tip, connate for over half their length, 8–12 mm long. Leaves with petiole 8–20 mm long, glabrous; blade elliptic, 6–12 by 2–3.5 cm, the apex acute to subacuminate, the base acute, the surfaces glabrous, drying mottled reddish brown and gray. Inflorescences terminal or upper-axillary panicles 2–6 cm long, 3-branched from base, bearing 30 to 60 flowers. Flowers with pedicel 2–7 mm long, glabrous; calyx broadly cup shaped, 1–2 mm long, glabrous; corolla tubular with narrow tube 1–2 cm long and 5 spreading lanceolate lobes 2–6 mm long, white, glabrous outside, villous within; stamens 5, epipetalous in middle of tube, included, the anther linear-oblong, 1.5–2.5 mm long, the filament ca. ½ as long as anther; style about as long as tube, stigma lobes 1.5–2 mm long.

Fruits ovoid, 10–13 mm long excluding persistent cuplike calyx, red at maturity, longitudinally ribbed when dry.

TYPIFICATION. *Psychotria xanthochlora* was based on *Reinecke 337,* collected in 1894 in the mountains above Laulii, Upolu, but this specimen has probably been destroyed. I have therefore designated *Christophersen 538,* which was collected near the type locality, as the neotype. Christophersen (1938) noted in his discussion of the species that this specimen closely agreed with the now-lost type specimen of Reinecke, which Christophersen saw in Berlin. The neotype is at BISH, with duplicates at K and US.

DISTRIBUTION. Endemic to Savaii and Upolu; understory tree in montane to cloud forest; 500–1520 m alt.

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** SAVAII: above Matavanu, *Christophersen 1994* (A, BISH, K, US, W), *2012* (A, BISH, US), *2013* (BISH, K); Papaafu Crater, *Christophersen 2725* (BISH), *2731* (BISH); Aopo-Gagamalae, *Christophersen 3441* (A, BISH, K, US); S of Maugaloa, *Vaupel 469* (B, BISH, K, M). UPOLU: above Saluafata, *Christophersen 526* (A, BISH). WITHOUT FURTHER LOCALITY: *Whitmee s.n.* (BM).

This species is most closely related to *Psychotria insularum,* particularly the narrow-leaved variant (recognized by Rechinger as var. *atroviridescens* and by Christophersen as var. *montanum*) but differs from this in having ovate to elliptic (vs. linear-lanceolate) stipules and longer corollas.

Reinecke 337, collected behind Laulii, Upolu, was not located.

20. **Psychotria insularum** A. Gray, Proc. Amer. Acad. Arts **4:** 45. 1860; Schumann, Bot. Jahrb. Syst. **25:** 687. 1898; Rech. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **85:** 199. 1910; Setchell, Publ. Carnegie Inst. Wash. **341:** 46. 1924; Lloyd & Aitken, Bull. Lloyd Libr. Bot. **33**(4)**:** 105. 1934; Christoph. Bernice P. Bishop Mus. Bull. **154:** 53. 1938; Yuncker, Bernice P. Bishop Mus. Bull. **184:** 65. 1945. Var. *typica* Hochr. Candollea **5:** 268. 1934. TYPE: Samoa, without further locality, 1839, *U. S. Expl. Exped. s.n.* (lectotype, here designated, US *67256*; isolectotypes, GH!, K!, US *67257*!).

Psychotria insularum var. *montanum* Christoph. Bernice P. Bishop Mus. Bull. **154:** 54. 1938. TYPE: Samoa, Savaii, forest above Salailua, 750 m alt., 1931, *Christophersen 2942* (holotype, BISH!; isotype, A!).

Psychotria insularum var. *aprica* Rech. Denkschr. Kaiserl. Acad. Wiss., Math.-Naturwiss. Kl. **85:** 199. 1910. TYPE: Samoa, Savaii, on lava flow at Safune, 1905, *Rechinger 1043* (holotype, W!).

Psychotria atroviridescens Rech. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **85:** 198. 1910; Hochr. Candollea **5:** 268. 1934. TYPE: Samoa, Upolu, above Utumapu, 1905, *Rechinger 502* (holotype, W!).

Psychotria tutuilensis Christoph. Bernice P. Bishop Mus. Bull. **154:** 59. 1938. TYPE: Samoa, Tutuila, top of Le Pioa, 500 m alt., 1935, *Christophersen 3485* (lectotype, here designated, BISH!).

Shrub or small tree 1–4 m tall. Young stems mostly glabrous, or rarely densely covered with reddish brown hairs; stipules linear-lanceolate with pair of linear lobes 1–2 mm long, connate for most of their length to form sheath, up to 24 mm long. Leaves with petiole 0.5–4 cm long, mostly glabrous; blade lanceolate,

ovate, or elliptic, 6–20 by 2–9 cm, the apex acute to submucronate, the base acute, the surfaces usually glabrous, often drying mottled reddish brown. Inflorescences 1 to 4 (rarely more) loosely branching, terminal or subterminal, several-flowered panicles 1–10 cm long. Flowers with pedicel 1–7 mm long, usually glabrous; calyx campanulate, 1–2 mm long, shallowly divided into 5 acute lobes; corolla tubular, 6–12 mm long, with 5 ovate lobes 2–5 mm long, white, glabrous on outside, densely pilose within; stamens 5, epipetalous in upper throat, included, the anther linear, 0.5–1.5 mm long, the filament ca. ½ as long as anther; style as long as tube, slightly exserted, stigma lobes 0.5–1 mm long. Fruits ovoid, 6–10 mm long excluding persistent calyx, shiny red at maturity, with 2 or 3 longitudinal ribs on each pyrene face when dry.

TYPIFICATION. Christophersen listed two specimens (*Christophersen 3485, 3521*) of his *Psychotria tutuilensis* as types, but this cannot be done. I hereby designate one of these syntypes, *Christophersen 3485* (BISH), as lectotype.

DISTRIBUTION. Indigenous to Tonga, Niue, Wallis, Futuna, and all islands of Samoa;[5] in Samoa common understory tree or shrub in coastal to cloud forest; near sea level to 1400 m alt.

LOCAL NAME AND USE. *Matalafi,* a well-known name in Samoa. This species is also sometimes called *lau mafatifati* or *fatifati,* meaning "brittle leaf," but these names also apply to *Geniostoma* spp., which are superficially similar (Whistler, 1984). The leaves are commonly used in Samoan medicines for treating "ghost sickness."

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** SAVAII: Taga, *Bristol 2220* (BISH, GH, K); above Matavanu, *Christophersen 836* (BISH, W), *2015* (A, BISH, US, W), *2047* (BISH), *2171* (BISH), *2197* (A, BISH, M, US); near Vaipouli, *Christophersen 1849* (A, BISH); behind Safune, *Christophersen 2433* (BISH); near Saleaula, *Christophersen 2464* (BISH); Safune-Aopo, *Christophersen 2493* (BISH); near Salailua, *Christophersen 2587* (BISH), *2590* (A, BISH, M, US), *2591* (BISH), *2592* (A, BISH, W), *3119* (BISH); near Taga, *Christophersen 2834* (A, BISH, K, US); Faala, *Cox 91* (GH); Faala-Tafuatai, *Cox 161* (BISH, GH, K); near Malo, *Rechinger 1109* (W), *1178* (W); Aopo-Asau, *Rechinger 1945* (W); Matautu, *Vaupel 66* (B, BISH, K, M, US, W, WRSL); Aopo, *Vaupel 175* (B, M); S of Maugaloa, *Vaupel 637* (B); above Ologogo, *Whistler 513* (BISH, BM, PTBG); above Asau, *Whistler 1746* (PTBG, US); Puapua-Saumalaeulu, *Whistler 2193* (PTBG). APOLIMA: *sine loco, Rechinger 268* (BM, W). MANONO: *sine loco, Rechinger 558* (W); behind Faleu, *Whistler 4509* (K, PTBG, US). UPOLU: Lefaga, *Bristol 1960* (BISH, GH), *1977* (BISH, GH), *2046* (BISH), *2485* (BISH, GH, K); "open forest on foothills," *Bryan 97* (BISH, K, M); above Malololelei, *Christophersen 2* (BISH), *195* (A, BISH), *237* (BISH, US); near Apia, *Eames 12* (BISH, US); near Vailima, *Eames 77* (BISH); Moamoa, *Eames 207* (BISH, GH); *sine loco, Funk 72* (BM); *sine loco, Graeffe 12* (BM), *31a* (HBG), *31b* (HBG), *47a* (HBG), *206, pro parte* (HBG), *212, pro parte* (HBG), *218* (HBG); Lanotoo, *Hochreutiner 3277* (G, GH (fragment)); Falefa, *Hochreutiner 3452* (G, GH (fragment)); Mt. Vaea, *MacDaniels 1117* (BISH); Toamua, *McKee 2906* (BISH); S coast at Aufaga, *McKee 2925* (BISH, E, K); Afiamalu, *McKee 2973* (BISH, E); above Vailele, *McKee 3004* (BISH); Mt. Vaea, *Rechinger 330* (W); near Safata, *Rechinger 555* (W); near Motootua, *Rechinger 569* (W); near Malifa, *Rechinger 572* (W); Lanotoo, *Rechinger 620* (W), *717* (W), *763* (BM, K, US, W); near Laulii, *Rechinger 1258* (W); above Vaisigano, *Rechinger*

[5]It is also reported from Hawaii on the basis of a Mann and Brigham specimen collected over 150 years ago (Sohmer, 1977), but the specimen is lost and the record doubtful.

1456 (W); near Samea, *Reinecke 85* (E, G); Tofua, *Reinecke 92* (G); Mt. Sigaele, *Reinecke 335* (G); *sine loco, Walter 2* (BISH); near Laulii, *Whistler 379* (B, BISH, PTBG, US); near Lanotoo, *Whistler 422* (PTBG, US), *423* (PTBG), *2176* (PTBG); Nuutele Is., *Whistler 467* (B, BISH, PTBG, US), *595* (BISH, PTBG, US), *3520* (PTBG); near Saaga, *Whistler 1110* (B, BISH, PTBG, US); Mt. Fiamoe, *Whistler 1165* (K, PTBG, US); Afulilo, *Whistler 1579* (PTBG); near Amaile, *Whistler 1835* (BISH, PTBG, US); Nuulua Is., *Whistler 1944* (BISH, K, PTBG), *4235* (BISH, PTBG), *4426* (K, PTBG, US); Fanuatapu Is., *Whistler 4411* (PTBG, US). TUTUILA: "forest on ridges," *Bryan 85* (BISH); Papatele ridge, *Christophersen 1009* (BISH); Matafao ridge, *Christophersen 1043* (BISH); Alava ridge, *Christophersen 1820* (A, BISH, US), *1826* (BISH); Le Pioa, *Christophersen 3521* (A, BISH), *3550* (BISH), *3557* (BISH), *3558* (BISH); Pago Pago, *Diefenderfer 11* (BISH); Goat Is., *Garber 792* (A, BISH); behind Pago Pago, *Garber 932* (BISH, US); Vatia trail, *Lamoureux 3007* (PTBG), *3012* (PTBG); *sine loco, Long 1983* (PTBG), *1990* (PTBG), *1994* (PTBG); Fagasa-Matafao, *Long 3065a* (BISH); Pago Pago reservoir trail, *Long 3086* (PTBG), *3102* (BISH, PTBG); behind Fagatogo, *Mitchell 506* (BISH); *sine loco, Mitchell 517* (BISH); Fagasa trail, *Setchell 82* (UC, US); behind Pago Pago, *Setchell 256* (GH, UC), *526* (UC), *572* (UC); Alava ridge, *Spense 484* (BISH); near Tafuna, *Whistler 1437* (BISH, G, PTBG, US); Aoloaufou, *Whistler 2737* (B, BISH, G, K, PTBG); Alava ridge, *Whistler 2767* (B, BISH, PTBG), *3638* (PTBG); near Matafao, *Whistler 3542* (PTBG); Le Pioa, *Whistler 3666* (PTBG), *3667* (PTBG); Pago Pago, *Wilder 17* (BISH), *78* (BISH); near Aua, *Wilder 47* (BISH); Tafuna, *Wisner 61* (BISH), *67* (BISH); Breakers Point, *Wisner 130* (BISH); above Pago Pago, *Yuncker 9350* (BISH). OFU: behind Ofu Village, *Yuncker 9444* (BISH), *9476* (BISH). TAU: Mt. Tau, *Cox 310* (BISH, GH, K); Fitiuta trail, *Garber 555* (A, BISH); behind Faleasao, *Garber 573* (BISH); near Laufuti, *Garber 768* (BISH, K); above Luma, *Whistler 1398* (G, PTBG); near Siufaga, *Yuncker 9008* (BISH); Fitiuta trail, *Yuncker 9060* (BISH). WITHOUT FURTHER LOCALITY: *Graeffe 85* (BM), *86* (BM), *97* (BM), *s.n.* (BM); *Whitmee 59* (MEL), *81, pro parte* (MEL), *122* (MEL), *126* (K).

This species is quite variable—enough so that Rechinger and Christophersen both described one other species and variety within the complex. The width of the broadest leaves of specimens collected from sea level to 300 m ranges from 5 to 9 cm, while that of the specimens from over 500 m is 2–3 cm. Based solely upon this difference, Christophersen described var. *montanum* comprising his specimens from the higher elevations. This appears to be the same as Rechinger's *Psychotria atroviridescens,* which would then be a synonym of var. *montanum.* Rechinger also named var. *aprica* from the lava flows of Savaii, but the differences noted are vegetative and minor and may be more a result of the lava substrate than of genetic differences. Christophersen recognized the individuals collected from the trachyte plugs of Tutuila (Le Pioa and Matafao) as constituting a distinct species, *P. tutuilensis,* but again, this taxon does not seem very distinct, at least at the species level, and may merely be an ecotype adapted to the impoverished soil on these two peaks.

There may, however, be one distinct variety: *Whistler 1835, Christophersen 2587, Christophersen 836,* and *Vaupel 175* have inflorescenses densely covered with erect, reddish brown hairs. This does not seem to be merely a geographic or edaphic variation because the specimens were collected on different islands (three on Savaii, one on Upolu), in different habitats, and from ca. 200 to 1000 m elevation. This character also appears on *Mackee 19909* (BISH), the single specimen of *Psychotria insularum* seen from Uvea (Wallis). Until I see more specimens from Uvea, I hesitate to recognize a variety formally.

Three specimens listed by Reinecke were not located and are probably lost.

These are *Graeffe 1608,* without further locality; *Reinecke 195,* collected at Mulifanua, Upolu; and *Reinecke 341,* from Lanoanea, Upolu.

Undetermined Species

Two of the specimens I saw could not be identified. *Graeffe 206, pro parte* (HBG), from Upolu, without further locality, and *Rechinger 147* (W), collected above Motootua, Upolu, but listed by Rechinger as *Randia* sp., appear to be identical, but both lack flowers. They probably belong to *Psychotria*—possibly to a new species—but are inadequate for description.

ACKNOWLEDGMENTS

I am greatly indebted to the faculty and staff of the herbaria that I visited and from which I borrowed specimens during the course of my work. I also wish to thank Dr. William Theobald, of the Pacific Tropical Botanical Garden, for his sponsorship of much of the research; Dr. A. C. Smith, of the same institution, for his helpful comments on some of the species; Dr. Harold St. John, of the Bishop Museum, for his help with the Latin descriptions; Dr. Gerald Carr, of the University of Hawaii Botany Department, for his assistance with the chromosome counts; and Dr. Cliff Smith, of the same department, for his help with the word processor used.

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MORPHOLOGY AND TAXONOMY OF THE NEW WORLD SPECIES OF MAIANTHEMUM (LILIACEAE)

JAMES V. LAFRANKIE, JR.[1]

This paper presents a morphological study, including a revised taxonomy, of the fifteen New World species of *Maianthemum* Wigg. and is preliminary to a world-wide taxonomic revision and phylogenetic analysis of the genus.

The species of *Maianthemum* can be divided into three geographically defined groups: North American, distributed from the arctic to just beyond the Rio Grande; Central American, growing from the state of Mexico to western Panama; and Eurasian, most of which are found in eastern Asia. Most species of *Maianthemum* are restricted to one of the three regions, and the centers of taxonomic diversity for the genus are in eastern and western Canada, Guatemala, and southern China. However, the present study is focused not so much on geography as it is on vegetative morphology, which is very diverse among the many species. A novel aspect is the emphasis placed on the individual shoot as the basic unit of form and growth. The first portion of the shoot, the rhizome, is given special attention, which is significant in two respects. Taxonomically, the rhizome exhibits numerous features that distinguish species decisively, often even when features of the leaves and flowers are ambiguous. Also, the rhizome is ecologically important because it is the perennial portion of the plant, an organ of nutrient and water storage, and the source of renewal buds that extend the life of the individual.

Maianthemum is clearly separated from allied genera in the tribe Polygonatae in having the combination of a simple aerial stem, a morphologically distinctive terminal inflorescence, spotting on immature berries, and a haploid chromosome number of 18. The clarity of the generic limits has been appreciated by only a few previous authors, and most modern floras divide *Maianthemum* into a pair of closely allied genera, *Maianthemum* and *Smilacina* Desf. The division is based on the number of floral parts: the 25 species with trimerous

[1]Harvard Forest, Petersham, Massachusetts 01366.

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flowers (six tepals, six stamens, three carpels) typical of the Liliaceae are placed in *Smilacina,* whereas the three species with dimerous flowers (four tepals, four stamens, two carpels) are placed in *Maianthemum* sensu stricto. Earlier (LaFrankie, 1986), I assembled comparative data for the genera in the Polygonatae and demonstrated that *Maianthemum* sensu lato is distinguished from all allied genera by a singular combination of morphological traits, including a unique karyotype, whereas the dimerous and trimerous species are separated from one another by only a single derived feature. I then recommended that *Maianthemum* and *Smilacina* be combined under *Maianthemum,* which is the older name. Despite the number of species involved and their familiarity to botanists of the Temperate Zone, the possibility of conserving the name *Smilacina* was rejected. The transfers did not obscure the older literature, nor did they complicate current taxonomic research, which is chiefly Neotropical and Asian. Therefore, in consequence of this broader—although still traditional—view, the present study is the first modern taxonomic work to treat both the dimerous and trimerous species under the same generic name.

Because some of the species in this genus are well known under the name *Smilacina,* a further note on the new combinations is appropriate. While it is possible that the dimerous species originated prior to the 25 trimerous species and thereby merit consideration as a distinct genus, there is no evidence to support such a scenario. Much to the contrary, it appears on morphological grounds that the dimerous species are most closely related to sympatric trimerous species of the North Temperate Zone. In vegetative form, growth habit, distribution, and inflorescence architecture, at least one trimerous species, *Maianthemum trifolium,* bears a greater resemblance to the dimerous species than it does to the large paniculate species of the Tropics. In summary, the evidence presented within this work and in the earlier note (LaFrankie, 1986) indicates that under no circumstances would the combination of the dimerous and trimerous species be discordant with phylogeny, but separation of the groups most likely would be. Other details of generic nomenclature are published in the earlier note (LaFrankie, 1986).

The nomenclatural history of the individual North American species is somewhat complicated because many generic synonyms have been published. By contrast, the taxonomic history of these species is relatively clear. In *Species Plantarum* Linnaeus (1753) recorded three of the five species now known from North America. He was probably unfamiliar with the dimerous species from the northwestern part of the continent, *Maianthemum dilatatum,* and he considered the dimerous plant of the northeastern section, *M. canadense,* to be conspecific with the Eurasian *M. bifolium* (L.) F. W. Schmidt. After the two dimerous species of North America were recognized during the early 1800's, the taxonomy of the species indigenous to temperate North America remained rather uncontroversial, except perhaps the work of Greene (1889), which contained several new species and dozens of manuscript epithets for *M. stellatum* and *M. racemosum* (discussed under the individual species). My treatment does not differ in any major point from the most recent studies (Galway, 1945; Ingram, 1966), other than in using new combinations based on *Maianthemum* for the trimerous species.

However, this paper does address several taxonomic issues concerning the species of *Maianthemum* in Central America. The monographic treatment of the genus by Baker (1875), under the name *Tovaria* Baker, is now much outdated, as is the revision of that work by Hemsley (1879–1888). The most recent taxonomic revision was by Emons (1945). Although his study was limited to herbarium material, he made good use of the collections of Standley and Steyermark from Guatemala, and his species descriptions—with the exception of the overly inclusive *Smilacina paniculata*—are generally sound. However, recent and extensive collections from Veracruz, Chiapas, Costa Rica, and Panama have provided numerous specimens that illustrate the difficulty of distinguishing among *Maianthemum scilloideum, M. flexuosum,* and *M. amoenum.* This paper clarifies the distinctions and also presents an analysis of the diverse plants with paniculate inflorescences.

MORPHOLOGY

Growth Habit

The identification of species in *Maianthemum* is based largely on the morphology of the floral shoot, knowledge of which requires an understanding of shoot development. The study of growth habit therefore plays an important role in the taxonomy of this genus. In *Maianthemum,* as in many monocotyledons, the fundamental unit of organization is the individual shoot axis. Each shoot is relatively short lived by virtue of its terminal inflorescence, but the life of the plant is extended indefinitely through the early development of renewal shoots from lateral buds located at the base of older shoot axes (see Figure 1). This serial replacement of short-lived determinate shoots is termed "sympodial growth" and is characteristic of all species of *Maianthemum,* as well as all other genera in the tribe Polygonatae. Despite the similarity of growth habit, the individual species differ markedly in morphological details.

Each shoot consists of three discrete portions: a rhizome, a leafy stem, and a terminal inflorescence. Although these sections are entirely distinct, they are not separate organs but represent different developmental stages of a single shoot. Each shoot commences with a rhizome that grows horizontally, carrying the apex clear of the parent shoot and then turning upward to produce the leafy portion. A terminal inflorescence completes the development; thereafter, the aerial portion usually abscises from the persistent rhizome portion. (A more detailed analysis of shoot morphology and development is presented in LaFrankie, 1984, 1985b.)

Maianthemum goes through a stage of establishment growth similar to that seen in other Liliaceae (Barton & Schroeder, 1942; Barton, 1944; LaFrankie, 1985a). Germination is hypogeal, the cotyledon remaining within the seed as the primary shoot axis develops at the cotyledonary node. The first foliar elements are scale leaves, followed by a single foliage leaf supported by an elongate petiole. Petiolate foliage leaves replace one another in succession as the primary seedling axis grows in diameter; ultimately, the primary axis produces a pair of sessile foliage leaves supported by an extended aerial stem, and

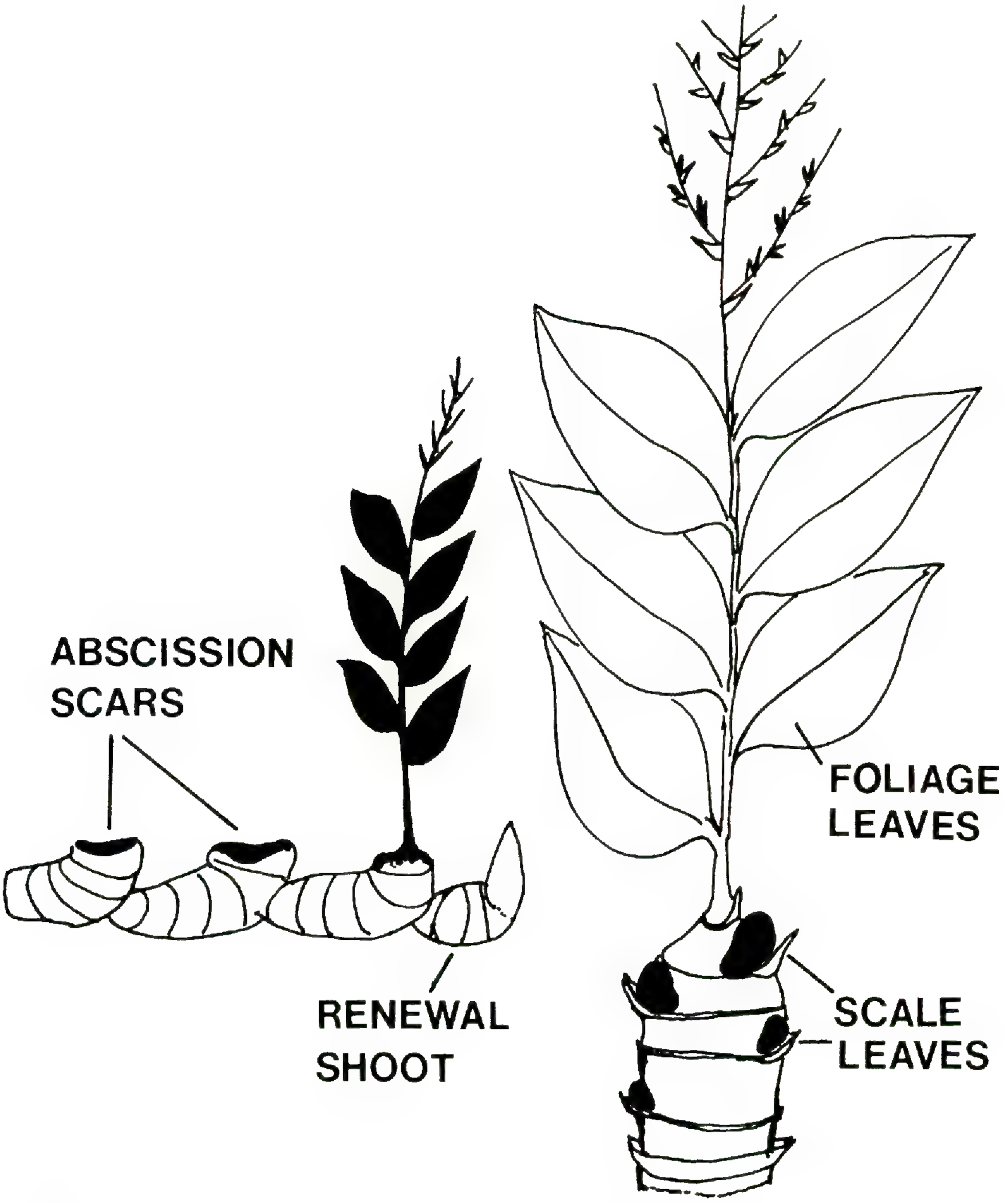


FIGURE 1. Shoot morphology in *Maianthemum*. Individual shoots determinate, growth through sympodial renewal; each shoot comprising persistent rhizome portion and short-lived aerial shoot (lost through abscission). Rhizome portion bears scale leaves, lateral buds ranked acropetally in size, and roots (not shown); aerial portion bears foliage leaves without axillary buds; inflorescence bears bracts subtending single flowers or extended racemes.

thereafter adult or renewal growth commences as renewal shoots are produced from axillary buds on the lower portion of the parent stem.

There are four different patterns of shoot development in *Maianthemum,* but they share several features. In all species of *Maianthemum,* the two growth processes of initiation and extension are separated temporally. All appendicular parts are initiated in miniature within a swollen renewal bud and then reach full size through uninterrupted meristematic growth and cell enlargement. In

the first type of growth, shoot development is both complete (meaning that all leaves and flowers are produced at once) and seasonal. This type of growth is typical of spring emergents of the Temperate Zone, such as *M. racemosum,* but it is also found in the seasonal environments of the tropical mountains, in which case the renewal shoot usually extends during the dry season (January–March). In the second type of growth, shoot development is also complete, but shoots are initiated more or less continuously and without strict regard to the season. This type is found in tropical plants of some lower montane areas in which seasonality is less pronounced. The third and fourth types of shoot growth involve intermittent rather than complete development. Among the New World species, only *M. trifolium* exhibits the third type of growth: a pair of petiolate foliage leaves is produced in the first growing season, and an extended floral stem bearing two to four sessile foliage leaves during the second. The fourth growth type is shown by *M. dilatatum* and *M. canadense*; it is quite similar to the third, differing in that only a single petiolate leaf appears during the first growing season. This vegetative phase may continue for as many as six subsequent growing seasons before a floral shoot is produced (Kana, 1983). That the third and fourth types of growth correspond in many details to the process of establishment growth (LaFrankie, 1985a) is perhaps indicative of their neotenic origin.

Roots

In *Maianthemum,* root meristems are initiated near the rhizome apex as part of primary growth, so the number of roots on a stem is fixed early in development—new roots cannot grow from old stems. This constraint is important since lost roots can be replaced only through the development of new rhizomes, which is a seasonal phenomenon for many species.

Roots in *Maianthemum* are of limited taxonomic significance. Their anatomy is quite uniform: each has a broad cortex lacking storage products, a sclerized pith lending mechanical support, and vessels in the xylem. Some species can be recognized by the dimensions of the roots and by their distribution along the rhizome. Normally, roots occur all over the rhizome at nodes and internodes and are especially numerous at the base of the leafy stem, but *M. stellatum* has dimorphic roots with many small roots scattered along the stem and a few larger ones aggregated near the shoot base, and *M. trifolium, M. canadense,* and *M. dilatatum* have roots restricted to the nodes.

Rhizome

In the past the term rhizome has been applied to various plant parts (see Holm, 1929; Bell & Tomlinson, 1980), often with little thought or regard for precise terminology. In the shoot system of *Maianthemum,* the rhizome is the perennial branching portion that bears roots, scale leaves, and lateral buds. The transition from rhizome to leafy stem is discrete and, in most species, clearly demarcated by a long internode commencing the aerial portion. The leafy stem is further distinguished in having an epidermis instead of a periderm, in having collateral instead of amphivasal vascular bundles, and in lacking

axillary buds and roots. In most species of *Maianthemum*, the rhizome portion of the shoot persists for several shoot generations, accumulating to form an often-extensive branching aggregate. In this paper I use "rhizome" to describe this sympodial aggregation, and "individual rhizome unit" to describe the rhizomatous portion of a single shoot.

In form and habit rhizomes in *Maianthemum* are diverse: in some species they are extended and stoloniferous, while in others they are swollen and tuberous; they may be subterranean, aquatic, or fully exposed; they may even be orthotropic as in *M. paludicolum*. Most species are easily distinguished by their rhizomes alone, using features such as number of scale leaves, distance between internodes, number of lateral buds and their plane of insertion, and type and distribution of storage products.

In general, scale leaves of the rhizome are distichous and are inserted in a plane parallel to the ground, although in fact the planes of insertion of right and left scale leaves form a slight dihedral angle toward the stem's lower side. Most often, lateral buds are axillary, but in some species they may be initiated in eccentric positions, toward either the midpoint of the internode or the lower side of the rhizome. This has the effect of creating a linear rather than a forking sympodium, a situation that also occurs in *Croomia* Torrey & A. Gray (Tomlinson & Ayensu, 1968) and *Podophyllum* L. (Holm, 1899). In all species of *Maianthemum*, the lateral buds are acropetally ranked in size, and usually the one or two buds nearest the foliar stem portion form the subsequent renewal shoots, while those more distal remain dormant.

The carbohydrate reserves of *Maianthemum* and their patterns of deposition are evidently quite diverse and merit a thorough investigation. With regard to the storage of starch (as identified microscopically and with IKI), I have made observations on fresh rhizomes in most species and have extended these observations using rhizomes preserved in FAA. In some cases material from only one collection site was available for study, but in all instances several plants could be compared. In all, I discovered four patterns of starch deposition within the genus. 1) Starch may be absent entirely from all portions of the rhizome, as in *M. gigas*. 2) If starch is abundant in the developing rhizome, it may be depleted slowly over the course of three or four years, after which the rhizome decays, as in *M. stellatum*. 3) Alternatively, starch in a developing rhizome may be depleted very quickly, even before the renewal bud fully forms, and then remain absent, replaced in part by a thick mucilage, as in *M. racemosum*. 4) Having been initially depleted, starch may again accumulate in the distal portions of the rhizome, first in the fully developed cortex and then across the entire central cylinder, as in *M. flexuosum*.

LEAFY STEM

The leaf-bearing portion of the stem is roughly similar—at least in general aspect—in all species of *Maianthemum*, and this can make identification of vegetative material difficult. Differences among species often include stem and leaf dimensions, but these vegetative differences can be obscured by the developmental stages through which growing individuals pass. As a plant grows,

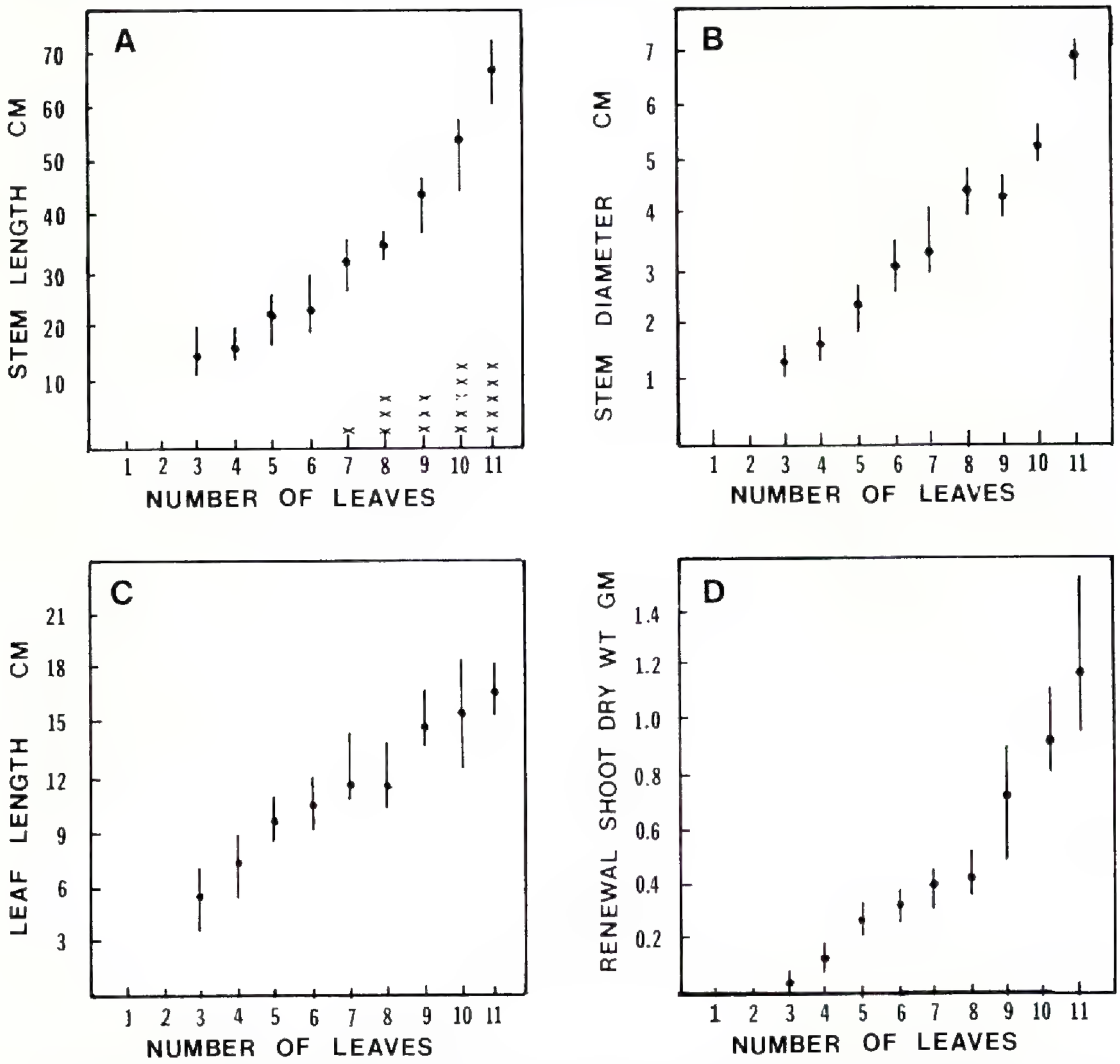


FIGURE 2. Relationship between morphometric features and number of foliage leaves on shoot (showing coordinated increase in size accompanying sympodial growth): A, length of aerial stem (reproductive individuals indicated by x's); B, aerial-stem diameter at base; C, length of the penultimate foliage leaf; D, dry weight of primary renewal shoot separated from base of aerial stem bearing indicated number of leaves. Data are mean and range of sample, indicating great constancy within each leaf-number class. Based on 5 randomly chosen individuals per leaf-number class, from natural population of *Maianthemum racemosum* subsp. *racemosum,* in Medford, Massachusetts.

larger shoots replace smaller ones, and the dimensions of the leaves and stem increase with each new shoot in a way that is consistent within a species. That is, for plants growing under more or less uniform conditions, there is a close correlation among morphometric features, including the number and dimensions of foliage leaves, the length and diameter of the stem, the dry weight of the renewal shoot, and the initiation of an inflorescence. In *M. racemosum,* for example, various morphometric features are closely correlated with the number of foliage leaves borne on a stem (see FIGURE 2). Due to the architectural similarity of the different species and the role that reduction has played in their evolution, small shoots of characteristically large species can sometimes be

confused with full-sized shoots of smaller species. A general rule of thumb is that a plant has not reached its full size until the inflorescence is longer than the penultimate foliage leaf.

In each species of *Maianthemum,* the leafy shoot has a characteristic habit or posture. The stem may be stiff and straight or slightly flexuous; it may be upright, pendent, or arching so as to display the foliage leaves in a plane. The habit can sometimes be useful in distinguishing between taxa, such as the upright and arching subspecies of *M. racemosum.*

The surface of the lower portion of the foliar stem is usually smooth and sometimes is even polished, whereas that of the upper portion may be sculptured with small ridges or distinct ribs sometimes bearing denticles or fine hairs. While the indument is rather variable within and among species of *Maianthemum* (as discussed under the section on leaves), the ribbing is a relatively consistent feature.

LEAVES

Foliage leaves in *Maianthemum* are simple and most often ovate, although they range from obovate or elliptic to almost lanceolate (distinctly cordate in *M. dilatatum*). Comparisons of leaf shape between species must be made between leaves taken from similar positions on the aerial stem, because leaf shape also varies along the length of a single shoot (see FIGURE 3). This precaution is particularly important with regard to the dimerous species since the two cauline leaves they bear are quite different from one another.

The leaf vasculature is similar to that of many other genera of tribe Polygonatae (Conover, 1982). A large median vein divides the leaf into equal halves, and each half is again divided by a vein of lesser strength. The four resulting panels are likewise equally divided and subdivided by ever finer parallel veins until panel widths of 0.8–2 mm are attained. Very fine commissural bundles then tie the parallel veins together. I term the pattern of venation in which adjacent parallel veins are of very different diameters as "veins ranked." This pattern differs from that shown by *Maianthemum stellatum, M. paludicolum,* and *M. trifolium,* in which adjacent parallel bundles are more nearly equal in strength, giving the leaves a striate appearance. This difference is the only taxonomic character associated with leaf venation. The reticulate venation found in the related genus *Prosartes* D. Don is not seen here, and distinctions based on three, five, or seven "main veins" are not tenable.

Hairs and denticles occur on the leaf, as well as on the main stem and the inflorescence axes. Hairs are always unicellular, pliable, and 80–300 μm long. Denticles protrude in two rows along each margin, most often near the apex. They may extend down the margin of the leaf to the base, sometimes also occurring along the veins on the abaxial surface and along the ribs of the stem and inflorescence. Denticles are approximately 20–80 μm long and are rounded or pointed, with the point directed outward or apically. The hairs and denticles in *Maianthemum* are no different from those found in other genera in the Polygonatae. Some previous authors (Butters, 1927; Fassett, 1935; Okuyama, 1935) have employed these fine features to distinguish taxa, usually at the

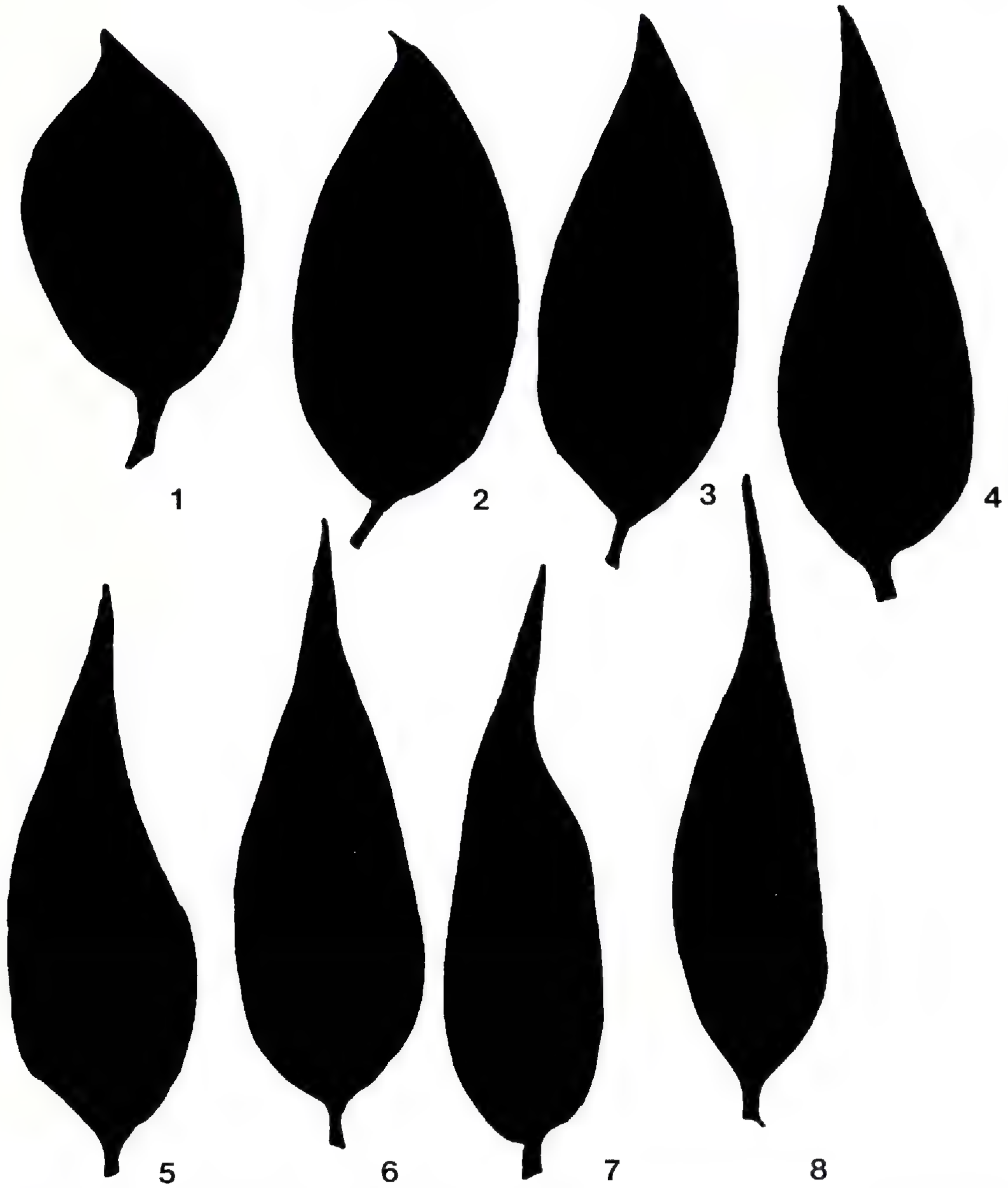


FIGURE 3. Leaf silhouettes from single stem of *Maianthemum septifolium* (*LaFrankie 84-V-19C*, GH), numbered from base toward apex.

varietal level, but I have not found them to be useful taxonomic criteria. Some species, such as the epiphytes *M. amoenum* and *M. macrophyllum,* which are glabrous and highly polished on all surfaces, are quite constant in these features. However, species such as *M. scilloideum* and *M. racemosum,* which typically have an indumentum, also include some totally glabrous individuals, as well as many others with intermediate levels of hairiness. My observations on both *Maianthemum* and other genera in the Polygonatae indicate that the presence or absence of these simple unicellular hairs is generally much too variable to justify the retention of forms or varieties based on this criterion alone.

INFLORESCENCE

The branching pattern in the inflorescence is the most useful feature by which to recognize species of *Maianthemum,* and I classify the inflorescences among four basic types. Three of these—panicles (main axis bearing lateral racemes at the nodes), complex racemes (main axis with two to seven flowers clustered at each node), simple racemes (main axis with a single flower at each node) (see FIGURE 4)—are found in New World species. The fourth type, found only in some Asian species (e.g., *M. henryi* (Baker) LaFrankie), consists of a main axis with flowers clustered at some nodes and fully extended racemes at one or two lower nodes.

Two fundamental and somewhat unusual features associated with lateral branches in the inflorescence are the apparent absence of both a basal prophyll (the first foliar element is a bract subtending a pedicel) and a terminal flower (the branch is morphologically indeterminate). These features are most clear in the large paniculate species, and less so in species with smaller, condensed inflorescences.

Analysis of the inflorescence is facilitated by locating the persistent bract that subtends every lateral axis. The bracts are usually small and scarious but are sometimes (as in the type specimen of *Smilacina racemosa* f. *foliosa* Marie-Vict., a synonym of *Maianthemum racemosum*) as large as small foliage leaves. Alternatively, the uppermost foliage leaf may be reduced to a small bract, thus giving the inflorescence a long peduncle, as in the type specimen of *S. racemosa* var. *cylindrata* Fern. (a synonym of *M. racemosum*).

Bracts associated with pedicels vary in position among the different species and can be a key feature in identifying herbarium specimens. In general, one bract subtends each pedicel (this is termed "basal" or "subtending"), but in *Maianthemum amoenum* it occurs at midlength along the pedicel. In *M. trifolium,* which has a simple raceme, each pedicel is subtended by one bract and may bear an additional bract either at its base or at its midpoint.

The evolutionary relationships among the different types of inflorescences may be complicated by both reduction and elaboration of the lateral racemes. One relationship that is rather clear at present is between some of the species with panicles and some with compound racemes. The inflorescences of many species (e.g., *Maianthemum scilloideum* and *M. septifolium*) are similar in miniature form within the resting buds, although they may differ in the number of flowers per node. As the leafy shoot expands, the lateral axes of the inflorescence may extend through uninterrupted meristematic growth as elongated racemes (as in *M. septifolium*) or remain compressed as dense fascicles (as in *M. scilloideum*). Even within a normally paniculate species such as *M. racemosum,* lateral axes sometimes fail to elongate, resulting in dense, columnar inflorescences. Such variants appear occasionally in *M. racemosum* throughout the United States and are especially common in Colorado.

One unusual feature of the panicle in *Maianthemum* is that the first one or two flowers on a lateral raceme are usually inserted directly at the base of the raceme. This position is attained because the internode below the pedicel fails to elongate, thereby isolating the first flower. Although the significance of this feature is uncertain, its constancy among many species is readily apparent.

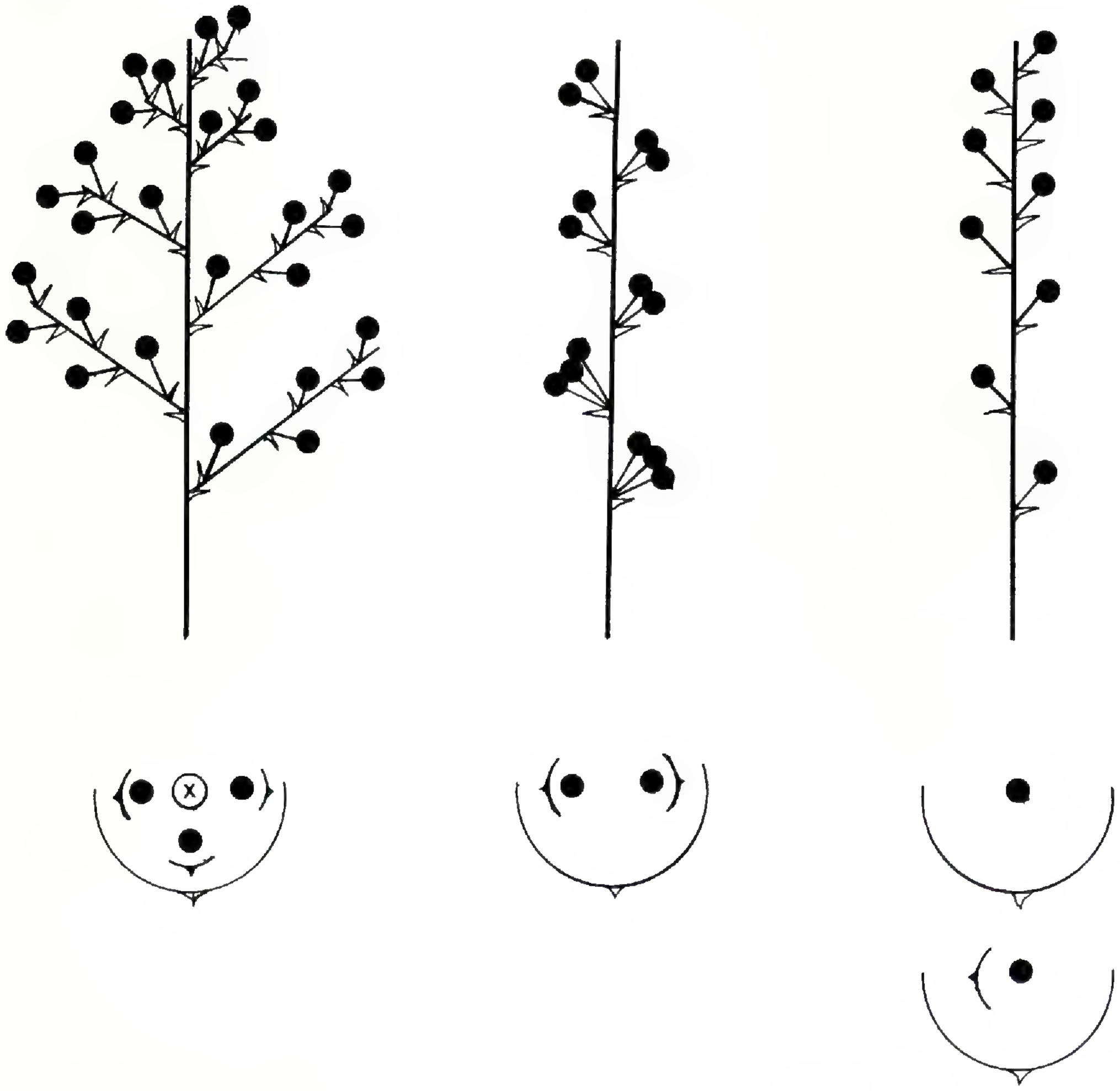


FIGURE 4. Schematic illustration of inflorescence architecture in New World species of *Maianthemum*. Lines = main axes, lateral axes, and pedicels; dots = flowers. Main and lateral axes indeterminate; prophyll lacking; all flowers subtended by bract; lateral axes usually arranged in helix but shown as distichous for clarity. Three types shown, with general view above, transverse view of individual lateral axis below: left, panicle with lateral axes racemes; center, complex raceme with lateral axes fascicles; right, simple raceme with lateral axes single flowers, sometimes with additional bract at base or near midpoint.

FLOWER

The flowers of *Maianthemum* are relatively small and inconspicuous and are characteristic of the lily family. They may be trimerous (six tepals, six stamens, three carpels) or dimerous (four tepals, four stamens, two carpels) through reduction (Utech & Kawano, 1976), but otherwise the flowers of different species are roughly similar to one another, differing chiefly in color, dimensions of parts, and disposition of tepals.

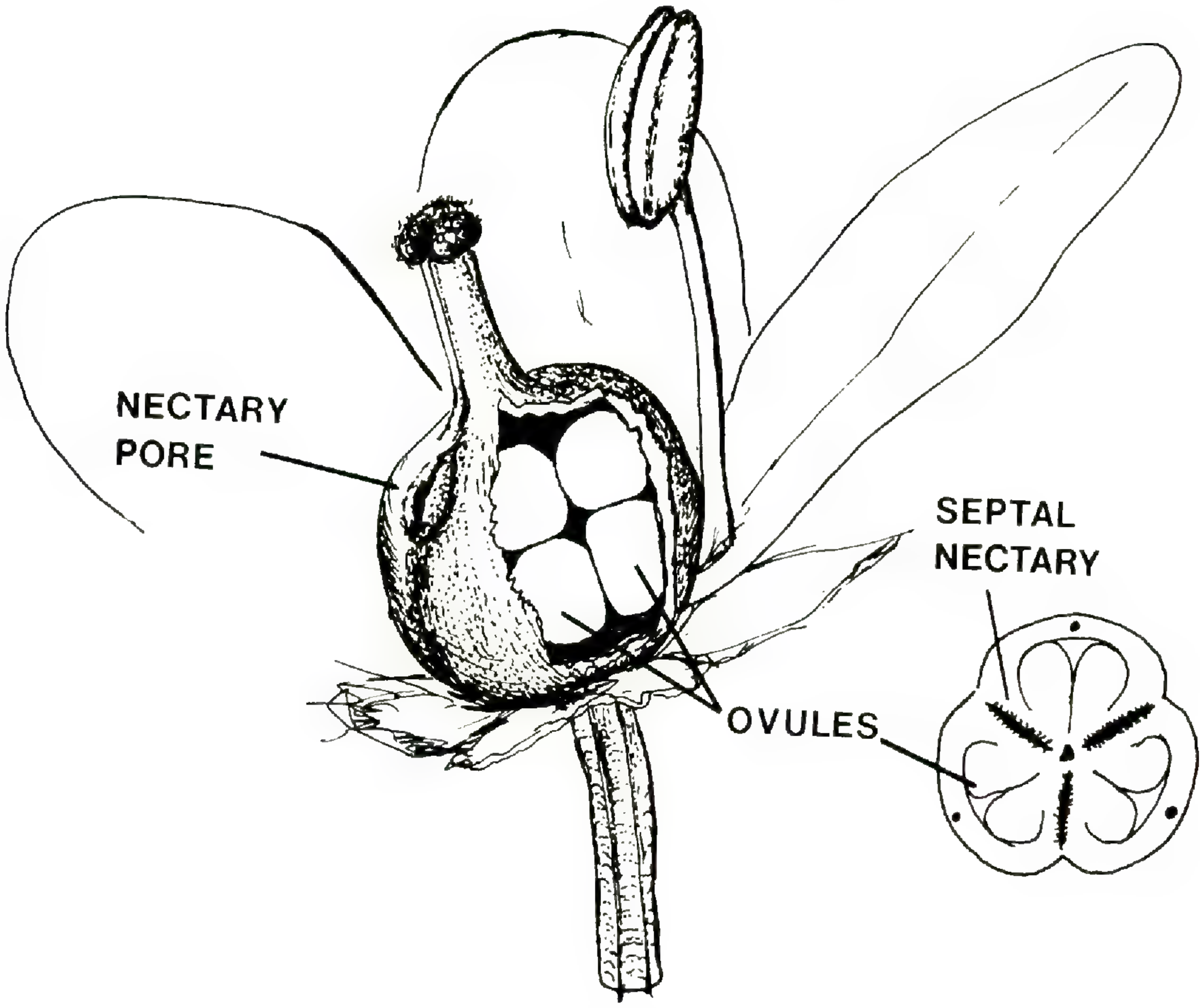


FIGURE 5. Floral morphology in New World species of *Maianthemum*: tepals free, more or less 2-ranked; stamens inserted near tepal base; nectary cells surrounding septal cavity; nectary pore with prominent lip; carpels with 1, 2, or 4 ovules.

The basic form of the flower is illustrated in FIGURE 5. The tepals are almost always uniform and are inconspicuously two-ranked. Among the New World species the tepals are always free, with the perianth spreading, reflexed, or cupuliform; in some Asian species such as *Maianthemum henryi,* the perianth is campanulate. The stamens are inserted at the base of the tepals or up to 1 mm above (as in *M. flexuosum*). The anthers are mostly cylindrical, tetralocular, and longitudinally dehiscent. According to Takahashi and Sohma (1983), the pollen of all New World species of *Maianthemum* is ca. 45 μm long, monocolpate, and with a reticulate exine.

The ovary varies in shape from spherical to cylindrical; the two or three carpels are weakly fused, and each has a single locule. The number of ovules in each carpel varies among the species from one to four but is most commonly two. All species have anatomically identical septal nectaries, although the prominence of the nectary pore varies, as does the volume of nectar exuded. In most species the exuded nectar is inconspicuous, but in *Maianthemum septifolium* the volume is so great that three very large drops accumulate at the junction of the three septal grooves and the adjacent stamens. The style is usually less than 0.5 mm wide and about as long as the ovary; the stigma is generally lobed and a little wider than the style. Seeds are more or less spherical, although in

some species with 12 seeds per fruit (e.g., *M. macrophyllum*), the seeds are conical with one or more flattened faces.

Seed diameter differs significantly among species but is not reliable in herbarium material because drying reduces the diameter from 20 to 40 percent. The seeds of all species are structurally uniform. The testa is thin and papery, straw colored or light brown. The endosperm is white, scaly, and rich in food reserves that are stored in the greatly enlarged cell walls. The embryo is always small and straight; the cotyledon can be spherical or claviform.

Most species of *Maianthemum* have snow-white flowers, but some have flowers infused with green or yellow, and others have them with flecks of red-violet. A few of the Central American species are more variable in flower color (including rose or lavender), but I have rejected the varietal ranking that Emons (1945) gave these individuals because color can vary through a whole range of shades even on a single plant.

CYTOLOGY

Chromosome number and morphology are uniform in most species studied to date (Therman, 1956; Kawano & Iltis, 1966; Kawano, Ihara, Suzuki, & Iltis, 1967; Valentine & Hassan, 1971; Sen, 1974). The haploid chromosome number is 18: one long (ca. 10 μm) with a metacentric constriction; nine medium-length, of which two have metacentric constrictions and seven have acentric or subterminal constrictions; and eight small (ca. 5 μm) with more or less metacentric constrictions. A few species show various levels of intraspecific polyploidy, but in general, evolution within this genus has been unaccompanied by gross chromosomal change.

ECOLOGY AND DISTRIBUTION

Most species of *Maianthemum* are forest herbs, but there are many exceptions, reflecting the broad ecological amplitude of the genus with regard to water, temperature, and light. For example, *M. stellatum* grows on sand dunes, *M. trifolium* and *M. paludicolum* occur in sphagnum bogs in full sun, and *M. amoenum* is found only as an epiphyte in the canopy of cloud forests.

Most of the species require cool temperatures and abundant moisture. In Central America *Maianthemum* grows in locations above 1500 m altitude that receive more than 1500 mm annual rainfall. The genus is generally hardy within these limits, and at least one species seems to be found in most of the areas where these two conditions are met.

Some of the ecological aspects of growth habit are mentioned above. Growth is generally episodic, with the phenological cycle closely tied to the seasons. The forest herbs of the Temperate Zone emerge in early spring, extending their foliage leaves before the forest canopy develops and then persisting through the remainder of the summer in light to moderate shade. In most of the tropical species, new shoots are extended between January and June, which coincides with the drier part of the year. This perhaps allows for more reliable pollination but also requires that water and nutrients be reserved within the rhizome. This constraint would apply all the more to the epiphytic species.

Little is known concerning the pollination biology of *Maianthemum*. My own observations indicate that the North American species are visited by a wide variety of small bees, flies, and beetles. The floral morphology of the tropical species also suggests general insect pollination, but two species may have specialized pollinators. The yellow-green flowers of the epiphyte *M. macrophyllum* are cupulate and open very slowly over a period of several weeks. The flowers of the terrestrial herb *M. flexuosum* are relatively large and usually lavender in color. The individual flowers are comparatively conspicuous (other species of *Maianthemum* gain their conspicuousness through aggregation of many tightly packed flowers in the inflorescence).

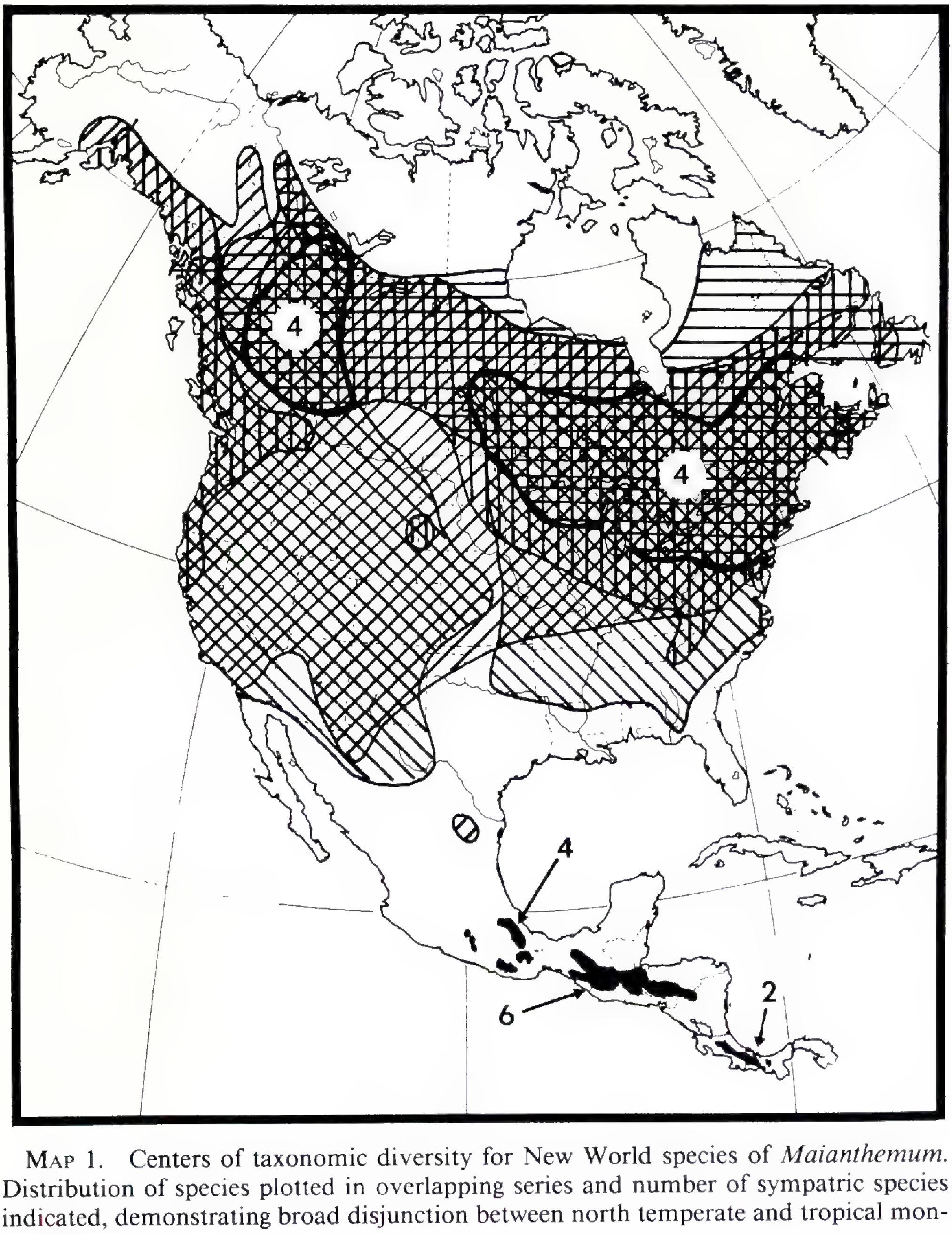
The breeding system in *Maianthemum* is also unknown. Two Asian species of *Maianthemum* (*M. hondoense* (Ohwi) LaFrankie and *M. yezoense* (Franchet & Savat.) LaFrankie) are reported to be dioecious, but their breeding systems have never been verified in the field (Kawano, pers. comm.). All species in the New World bear perfect flowers, but whether or not cross-pollination is required is not known.

In general, the species of *Maianthemum* are distinct and easily recognized. The four species in eastern Canada, for example, show absolutely no intergradation; they are thoroughly distinct, could never be confused, and evidently never hybridize in the wild. The species of Central America are relatively constant in the more critical morphological features, but they tend to be much more variable than the North American ones in leaf color, texture, and indumentum, as well as in other minor features. This may be due in part to the isolated and discontinuous population structure of species in the region, brought about by the highly dissected topography.

As mentioned in the introduction, the continental distribution of the genus (see MAP 1) shows a major discontinuity between the Rio Grande and the state of Mexico, with centers of specific diversity in Guatemala (6 species) and eastern and western Canada (4 species)—a truly remarkable disjunction. Whereas many related genera (such as *Clintonia* Raf.) show Asian-American disjunctions, and others such as *Streptopus* Rich. extend southward to the Asian tropics, *Maianthemum* is the only genus of tribe Polygonatae to be represented in the Neotropics.

The distribution of *Maianthemum* within Central America conforms to the general pattern exhibited by other montane taxa. It is bounded to the north by the arid regions of central Mexico and to the south by the lowlands of eastern Panama. Between these boundaries it has three centers of concentration: Veracruz-Oaxaca, Chiapas-Guatemala, and Costa Rica–Panama. These regions are separated from one another by the relatively broad expanses of the Isthmus of Tehuantepec and the lowlands of southeastern Nicaragua.

Maianthemum shares a pattern of distribution with those genera of the North Temperate Zone that have representative species in the tropical mountains, but there has been little work on just how these species came to occupy a tropical environment. In particular, the time of introduction of the northern elements into the tropical mountains remains a source of debate. The suggestion by Deevey (1949) that the North Temperate taxa arrived during the Pleistocene in response to glacial advance has been much criticized (Braun, 1955; Martin & Harrell, 1957; Graham, 1973). Earlier, Braun (1950, p. 486) had suggested



Map 1. Centers of taxonomic diversity for New World species of *Maianthemum*. Distribution of species plotted in overlapping series and number of sympatric species indicated, demonstrating broad disjunction between north temperate and tropical montane species.

that, "The warmth of the Eocene and Oligocene epochs may have resulted in withdrawal of temperate forms to high elevations, in eastern United States and in Mexico. During the Pliocene, a climatic barrier—the dryness of the Plains—developed. Even if withdrawal to higher elevations was accomplished earlier, a final separation would have been effected by the climatically dry belt, and contemporaneously with the late Tertiary shrinkage of mesophytic floras." An early date of immigration (pre-Miocene) into Central America would help explain the parallels between species of Old World and New. New World species

would be polyphyletic and would represent several successive periods of immigration from Asia, the first (Central American species) occurring in the early Cenozoic, and the last (boreal species) during the Neogene.

Studies by Miranda and Sharp (1950) and Steyermark (1950) have emphasized that genera found in both the North Temperate Zone and the Central American mountains are of two biogeographic types. One group consists of closely related species pairs or varieties; *Liquidambar* L. is an example often cited. The other group comprises species endemic to Guatemala and southern Mexico with nearest relatives in the western United States and eastern Asia; oaks are mentioned as examples of this type. *Maianthemum* falls more readily into the latter group; the species of Central America with large panicles, spherical rhizomes, and axillary lateral buds share more features with some species of Japan and China than they do with those of eastern Canada. However, the Asian species should be carefully studied in the field before any significant conclusions concerning their phylogenetic relationships are reached.

METHODS AND SPECIMEN CITATION

Specimens at A, BR, CAN, CAS, CR, DS, DUKE, F, GH, GOET, K, LL, MEXU, MICH, MO, MSC, NEBC, NY, ORE, PH, TENN, TEX, TRT, UC, US, WAT, WIS, WS, WTU, and XAL were annotated during the course of this study. Additionally, photocopies or single specimens were examined from DAO, FI, FTG, KNK, LSUS, MT, and WVA.

Species descriptions are arranged alphabetically; they are based on the examination of approximately 6000 North American and 1400 Central American specimens. Additionally, I was able to collect and cultivate living specimens of all taxa except *Maianthemum dilatatum, M. gigas* var. *crassipes, M. racemosum* subsp. *amplexicaule,* and *M. salvinii.* Additional materials of rhizomes and flowers were preserved in FAA for study in the laboratory.

The infraspecific taxa I recognize are in accordance with generally accepted definitions. They are morphologically distinct from one another and represent either geographically well-defined variants (ranking of subspecies), or scattered, isolated, or sympatric variants (ranking of varieties).

I have omitted specimen citations from the account of the North American species except in the case of type specimens, or to document limits of geographic distribution. A complete list of annotated specimens for the Central American species is provided. These are arranged geographically, from northwest to southeast. Duplicates are arranged alphabetically.

Distribution maps for the North American species, which are well known and have a continental distribution, were handled somewhat differently than those for the Central American ones, some of which are new and are more narrowly distributed. For the North American species I plotted the distribution upon an arbitrarily positioned grid in which each unit is 40 km on a side. Many western and Canadian specimens that are located only to county or province must be rejected by this method, but the resulting maps are uniform in meaning. Published distribution records, which are reliable and based on herbarium specimens, are included in the description but are not placed on the maps. References for the county distribution maps include Deam (1940); Steyermark

(1963); Braun (1967); Radford, Ahles, and Bell (1968); Voss (1972); Barkley (1977); Harvill, Stevens, and Ware (1977); Mohlenbrock and Ladd (1978); and Wherry, Fogg, and Wahl (1979). Within Central America specific collection sites are plotted only when they can be located precisely (i.e., when the site can be confidently located beneath the map symbol used to denote the taxon).

TAXONOMY

Maianthemum G. Weber ex Wigg. Prim. Fl. Hols. **14:** 29. 1780, nomen conserv. TYPE SPECIES: *M. convallarium* Wigg., nomen illegit. (= *Convallaria bifolia* L., *M. bifolium* (L.) F. W. Schmidt).

Unifolium Ludwig, Inst. Regn. Veg. ed. 2. 124. 1757, nomen rejic. TYPE SPECIES: *U. bifolium* (L.) E. Greene (= *Convallaria bifolia* L.).

Vagnera Adanson, Fam. Pl. **2:** 496. 1763, nomen rejic. TYPE SPECIES: *V. stellata* (L.) Morong (= *Convallaria stellata* L.).

Valentinia Heister ex Fabr. Enum. ed. 2. 37. 1763, nomen illegit. (incl. type of *Unifolium* Ludwig, 1757, nomen rejic.).

Polygonastrum Moench, Methodus, 637. 1794, nomen rejic. TYPE SPECIES: *P. racemosum* (L.) Moench (= *Convallaria racemosa* L.).

Sciophila Wibel, Prim. Fl. Werth. 147. 1799. TYPE SPECIES: *S. convallarioides* Wibel, nomen illegit. (= *Convallaria bifolia* L.).

Smilacina Desf. Ann. Mus. Natl. Hist. Nat. **9:** 51. 1807, nomen conserv. TYPE SPECIES: *S. stellata* (L.) Desf. (= *Convallaria stellata* L.).

Styrandra Raf. Amer. Monthly Mag. Crit. & Rev. **2:** 266. 1818. TYPE SPECIES: *S. bifolia* (L.) Raf. (= *Convallaria bifolia* L.).

Sigillaria Raf. *ibid.* **3:** 100. 1818 (= *Smilacina* Desf.).

Asteranthemum Kunth, Abh. Königl. Akad. Wiss. Berlin **1848:** 33. 1850. TYPE SPECIES: *A. vulgare* Kunth, nomen illegit. (= *Convallaria stellata* L.).

Medora Kunth, *ibid.* 34. TYPE SPECIES: *M. divaricata* Kunth, nomen illegit. (= *Smilacina fusca* Wallich).

Jocaste Kunth, Enum. Pl. **5:** 154. 1850. TYPE SPECIES: *J. purpurea* (Wallich) Kunth (= *Smilacina purpurea* Wallich).

Maia Salisb. Gen. Pl. 64. 1866. TYPE SPECIES: *Convallaria bifolia* L.

Neolexis Salisb. *ibid.* TYPE SPECIES: *Convallaria racemosa* L.

Tovaria Necker ex Baker, J. Linn. Soc., Bot. **14:** 564. 1875, non Ruiz & Pavón, 1794. TYPE SPECIES: *T. racemosa* (L.) Baker (= *Convallaria racemosa* L.).

Oligobotrya Baker, Hook. Icon. Pl. **16:** 1537. 1886. TYPE SPECIES: *O. henryi* Baker.

Terrestrial, aquatic, or epiphytic herbs, 10 cm to 2.5 m tall. Rhizome fleshy, persistent, densely clumped with units subspherical, or spreading with units filiform. Leafy stem pendent, leaning, or upright, with 2 to 17 foliage leaves distichously arranged. Leaves simple, clasping or with short petiole (or, in some dimerous-flowered species, long petiole); blade usually ovate, the base rounded, the apex acute to caudate, the margin flat or undulate, denticulate or not, the surfaces glabrous or pubescent. Inflorescence terminal, a panicle or raceme, with 15 to 400 flowers, lateral branches or fascicles distichous or in helix. Flowers usually perfect (some Asian species reportedly dioecious), trimerous or dimerous; pedicel usually subtended by bract; perianth spreading, cupuliform, or campanulate; tepals usually uniform, ovate, obovate, or triangular, 0.5–11 mm long, usually white (also lavender to red, or green); stamens inserted

at tepal base, the anther tetralocular, introrse; ovary with 2 or 3 carpels, septal walls with nectaries, the style usually less than 1.5 mm long, the stigma 2- or 3-lobed, usually less than 1 mm broad. Fruits usually lobed, 4–12 mm broad, with 1 to 12 seeds; seeds usually spherical, 3–6 mm in diameter, with thin, pale brown testa and scaly endosperm. Chromosome number $2n = 36$ most commonly reported.

KEY TO THE NEW WORLD SPECIES OF MAIANTHEMUM

1. Inflorescence a panicle.
   2. Lateral inflorescence axes > 2 cm long, spreading or slightly ascending; pedicels usually perpendicular to lateral axis, with bract subtending, longest pedicel < 7 mm; perianth spreading.
      3. Rhizome epidermis replaced by corky periderm; tepals conspicuous, > 2 mm long; Meso-America.
         4. Rhizome fleshy, cylindrical to subspherical, < 10 cm long, plagiotropic; foliage leaves with veins ranked in strength; terrestrial or epiphytic.
            5. Rhizome > 1.5 cm broad; leafy stem > 1 m long; foliage leaves 12 to 18.
               6. Plant 1.5–2.5 m tall; individual rhizome units broad-claviform to subspherical, 3–5 cm in diameter; inflorescence dense, with flowers inserted on lateral axes at 3–4(–10) mm intervals. . . 5. *M. gigas.*
               6. Plant 1–1.5 m tall; individual rhizome units short-cylindrical to narrow-claviform, 2–4 cm in diameter; inflorescence diffuse, open, with flowers inserted on lateral axes at intervals of (7–)10–20 mm. . . . . 9. *M. paniculatum.*
            5. Rhizome < 1.5 cm broad; leafy stem < 1 m long; foliage leaves 6 to 8 (to 10). . . . . 13. *M. septifolium.*
         4. Rhizome woody, narrow-cylindrical, much elongated, > 20 cm long, upright; foliage leaves with veins of uniform strength; in alpine bogs. . . . . 8. *M. paludicolum.*
      3. Rhizome epidermis persistent, yellow-brown, waxy; tepals inconspicuous, 0.5–1 mm long; North America. . . . . 10. *M. racemosum.*
   2. Lateral inflorescence axes < 2 cm long, sharply ascending; pedicels drawn toward main inflorescence axis, the bract not subtending, usually located near midpoint of pedicel; longest pedicel > 15 mm; perianth cupuliform; Meso-America.
      7. Inflorescence upright, 4–6(–9) cm long; fruit subspherical, 5–8 mm broad. . . . . 1. *M. amoenum.*
      7. Inflorescence pendent, 15–20 cm long; fruit 3-lobed, 10–12 mm broad. . . . . 7. *M. monteverdense.*
1. Inflorescence a simple or complex raceme.
   8. Individual rhizome units cylindrical, 1–30 cm by 1–2 mm; roots restricted to nodes; epidermis persistent, waxy; floral shoot with 2 to 4 foliage leaves; North America.
      9. Base of cauline leaf with narrow or broad sinus; inflorescence a complex raceme, 1 to 3 flowers per node; flowers dimerous.
         10. Plant 10–25 cm tall; upper cauline leaf ovate, sessile, the base with narrow sinus; lower cauline leaf cordate, with petiole 1–7 mm long; flowers 1 to 3 (usually 2) per node. . . . . 2. *M. canadense.*
      10. Plant 20–45 cm tall; upper cauline leaf triangular to cordate, with short petiole, the base with broad open sinus; lower cauline leaf deeply cordate, with petiole 7–10 cm long; flowers 1 to 4 (usually 3) per node. . . . . 3. *M. dilatatum.*

9. Base of cauline leaf tapered; inflorescence a simple raceme; flowers trimerous. ..... 15. *M. trifolium.*

8. Individual rhizome units cylindrical to claviform, 3–50 cm by 5–30 mm; roots at nodes and internodes; epidermis not persistent; floral shoot with 6 to 11 foliage leaves.

11. Vegetative surfaces glabrous, polished; perianth cupuliform; epiphytic; Meso-America.

12. Inflorescence upright or arched upward; pedicels stiff, reflexed, 4–9 mm long. ..... 6. *M. macrophyllum.*

12. Inflorescence pendent; pedicels spreading or drooping, 15–20(–30) mm long. ..... 11. *M. salvinii.*

11. Vegetative surfaces glabrous or pubescent, not polished; perianth spreading; terrestrial.

13. Individual rhizome units with internodes uniformly extended; roots uniform; inflorescence a complex raceme; Meso-America.

14. Inflorescence upright, main axis straight or slightly flexuous; longest pedicel 3–4.5 mm long; fruits usually spherical. ..... 12. *M. scilloideum.*

14. Inflorescence pendent, main axis strongly flexuous; longest pedicel 8–21 mm long; fruits strongly 3-lobed. ..... 4. *M. flexuosum.*

13. Individual rhizome units with 2nd and 3rd internodes greatly extended; roots dimorphic; inflorescence a simple raceme; North America. ..... 14. *M. stellatum.*

1. **Maianthemum amoenum** (H. L. Wendl.) LaFrankie, Taxon **35:** 588. 1986. FIGURE 6, MAP 2.

Smilacina amoena H. L. Wendl. Allg. Gartenzeitung **18:** 137. 1850. TYPE: Guatemala, Totonicapán, road between Los Encuentros and Totonicapán, 3100 m, 1 April 1977, *D. Smith & Clancy 553* (neotype, here chosen, F!).

Epiphytic herb, 0.5–0.8 m tall. Roots uniform, 8 to 12 per rhizome unit, evenly scattered, 20–60 cm by 1.2–1.8 mm. Rhizome densely clumped, the individual units subspherical, 3–5 cm broad, the scale leaves 6 or 7, the internodes 2–3 mm long, the lateral buds 4, axillary, 1 or 2 developing leafy shoots; epidermis replaced by periderm; starch present only near rhizome apex. Leafy stem leaning or upright, 25–40 cm long, 5–9 mm broad at base, the surface smooth, polished; foliage leaves 6 to 9 (to 11); internodes 2–5 cm long, shorter apically. Leaves clasping (some Mexican specimens with petiole 2 mm long); blade ovate, 6–13 by 2.5–5.5 cm, the apex acute or short-acuminate, the base rounded, the margin flat, denticles inconspicuous and appressed, the veins ranked, the surfaces glabrous, polished. Inflorescence a panicle (sometimes appearing subpaniculate when immature) with 25 to 75 flowers; main axis upright, stiff, straight, 4–6(–9) cm long, 1.5–2.5 mm broad at base, smooth, flattened, red, or white to pink with red patches, glabrous; internodes 1.5–4 mm long (lower ones 1–10 mm); lateral branches arranged in helix, sharply ascending, spreading as flowers bloom, each 1–2 cm long with 3 to 5 flowers, of which 1 inserted at branch base and others at ca. 4 mm intervals. Flowers trimerous; pedicel 12–20 by 0.7–1 mm, weakly ribbed or smooth, with bract inserted between base and midpoint; perianth cupuliform, the tepals uniform, 3.5–6.5 by 1.5–2.5 mm, lavender, or white infused with pink; stamens inserted

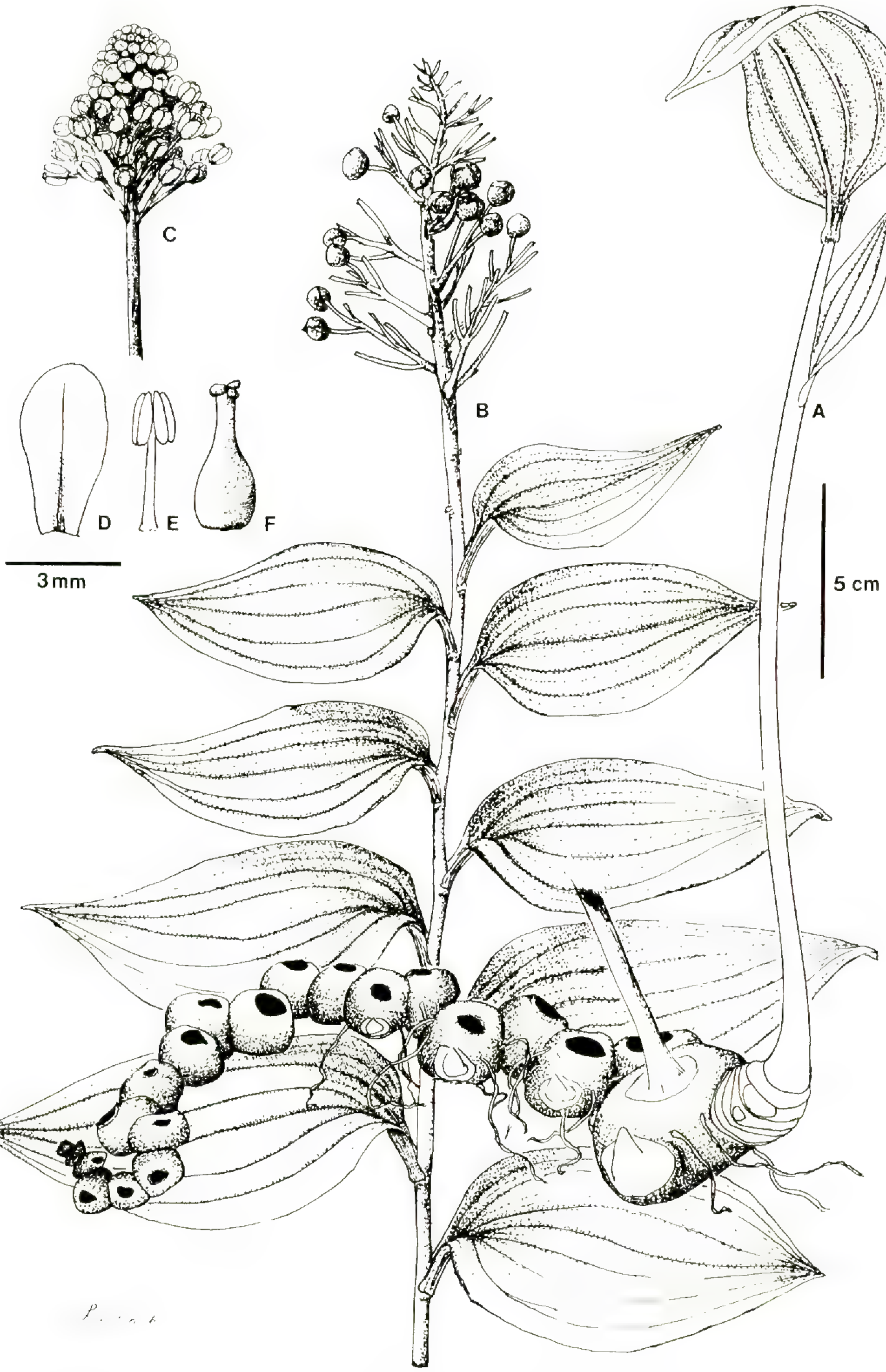
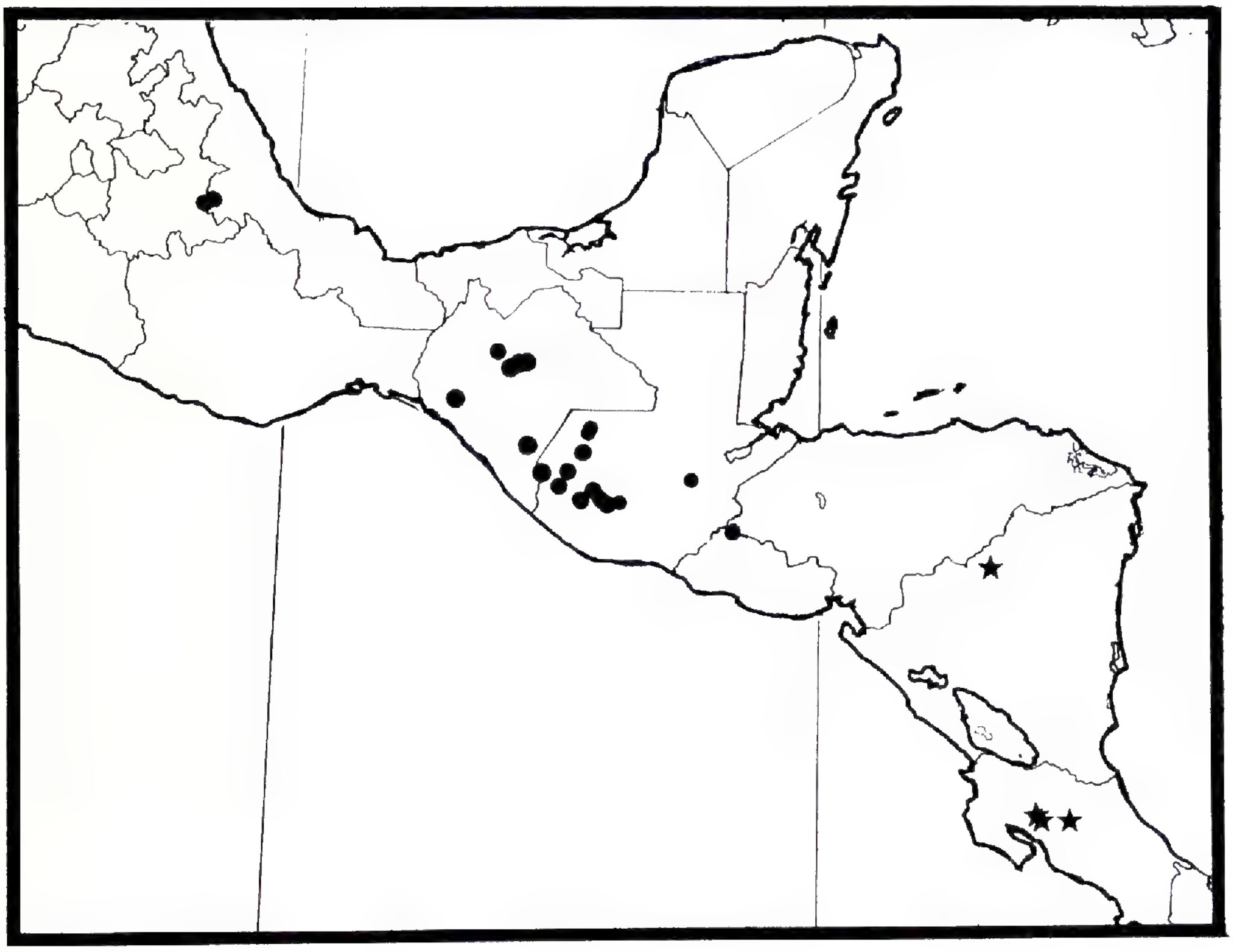


FIGURE 6. *Maianthemum amoenum*: A, rhizome and lower portion of leafy shoot; B, upper portion of leafy shoot and infructescence; C, inflorescence; D, tepal; E, stamen; F, ovary. (A, B based on *LaFrankie 84-V-21A*, GH; C–F on *Standley 61123*, F.)



Map 2. Distribution of *Maianthemum amoenum* (dots) and *M. monteverdense* (stars).

at tepal base, the filament 1.5–2 mm long, thin, the anther 0.5–0.8 mm long; ovary spherical to cylindrical, 1–1.5 by 1 mm, the style 1–1.5 mm long, the stigma distinctly 3-lobed, ca. 0.7 mm broad. Fruits spherical to weakly 3-lobed, 5–8 mm broad, green when young, maturing to red; seeds up to 12, slightly flattened, 3–4 by 2–3 mm. Chromosome number not known.

Ecology and distribution. Occasional; epiphytic at height of 5–15 m or more above ground, although sometimes persisting in blowdowns; often in dense clumps covering *Quercus, Drimys,* and other canopy trees of cloud forest; 2300–3300 m alt. New shoots developing annually; flowering January–April; fruits retained through October.

Northern limit in Veracruz; occasional in northern highlands of Chiapas, Sierra Madre del Sur, and Cerro Tres Picos, east through Guatemala (where somewhat more common); rare in El Salvador.

Specimens examined. **Mexico.** Veracruz: Nogales, 1500 m, *Matuda 1154* (GH, MICH, MO, US); Acultzingo, *Ugent 2372* (WIS). Chiapas: vic. Tenejapa, *Ton 889* (DS, LL, NY); El Triunfo, *Xolocotzi x-456* (MEXU); Pueblo Nuevo Solistahuacán, *Zuill 586* (DS); Cerro Hueytepec, *Alexander 1218* (MICH, NY), *Breedlove 26256* (DS, MO), *Carlson 1681* (F), *Laughlin 136* (DS, LL), *1026* (DS, F, US); Cerro Zontehuitz, 9300 ft, *Breedlove 9588* (DS), *14522* (DS, LL, WIS); Cerro Mozotal, *Breedlove 22723* (DS); SE side Cerro Tres Picos [in Sierra Madre del Sur], *Breedlove 34417* (DS); Malé-Motozintla, *R. Hernandez 398* (MEXU); Siltepec, *Matuda 15268* (F, MEXU). **Guatemala.** Huehuetenango: vic. San Mateo Ixtatán, *Breedlove 8929* (DS), *8939* (F); Paquix, Alto Cuchumatanes, *Holdridge 2291* (US). Quiché:

no further location, *Aguilar 1228* (F). QUEZALTENANGO: SE of Palestina, *Standley 84303* (F); Volcán Zunil, *Steyermark 34685* (F); 31 mi E of Quezaltenango, *S. White 5409* (MICH). TOTONICAPÁN: Cumbre del Aire, *Hunnewell 17108* (GH); between Los Encuentros and María Tecún, *Molina 15942* (F); between Los Encuentros and Totonicapán, *D. N. Smith 553* (F). SOLOLÁ: Volcán Santa Clara, *Steyermark 46876* (F). SAN MARCOS: above San Marcos, *Bunting 346A* (DUKE, NY, US); Volcán Tajumulco, *Plowman 3040* (GH), *3049* (LL); between Sibinal and Cajula, *Steyermark 36024* (F). CHIMALTENANGO: Caldera, *J. Johnston 1109* (F); vic. Tecpán, *Collin 21* (US), *Hunnewell 14654* (GH), *J. Johnston 633* (F), *Skutch 232* (US), *Standley 61123* (F). EL PROGRESO: between Finca Piamonte and Volcán Santa Luisa, *Steyermark 43553* (F). **El Salvador.** SANTA ANA: E slope La Esesmile, *Tucker 1033* (F, LL, MICH, NY, PH, UC, US).

A neotype of *Maianthemum amoenum* is required because I can find no specimen of the single cultivated plant used by H. L. Wendland in writing his description. The plant was collected in Guatemala, and its rhizome was sent to Göttingen with a shipment of orchids in 1845; most likely no specimen was made. While searching for an appropriate neotype, I located two specimens collected in Costa Rica by Wendland's son in 1857, seven years after the publication of *Smilacina amoena*. The annotations differ in the spelling of the location, one citing Volcán Berba, the other Volcán Yerba. They were probably both from Volcán Barba (Heredia Province). The younger Wendland was in Göttingen for several years just prior to leaving for Costa Rica, and he probably saw the plant described by his father. It is also quite likely that his father examined the Costa Rican specimens of *Maianthemum* and perhaps even compared them with the cultivated plant. Therefore, one would think these specimens should give a good impression of the plant H. L. Wendland described.

Unfortunately, these two specimens are quite different from the species to which the name *Maianthemum amoenum* has conventionally been applied. When H. L. Wendland's description (there was no illustration) is compared with these Costa Rican specimens, it is clear that the younger Wendland erred in his annotation and that the Costa Rican material does not belong to the species his father described. There are several key disagreements between the protologue and the specimens. According to the description, the leaves are somewhat clasping and have polished surfaces; the lateral racemes of the inflorescence bear four or five flowers with pedicels up to 18 mm long, drawn together in an upward-arching array. In the specimens from Costa Rica, the leaves are glabrous but not polished, and they have distinct petioles 4–5 mm long; the lateral racemes of the inflorescence are spreading, with pedicels 6–6.5 mm long and usually perpendicular to the lateral axis. Accordingly, I have annotated the Wendland specimens *M. gigas* and have chosen a modern representative specimen to serve as the neotype.

An unusual feature of *Maianthemum amoenum* is the great number of raphide crystal sacs that develop in the rhizome. In most species of *Maianthemum*, such sacs are a conspicuous cell type but are never very numerous. However, here they are a dominant feature of the histology. Each sac has a large vacuole that contains a bundle of unusually minute raphide crystals. Additionally, each vacuole is filled with mucilage and surrounded by a hard outer shell that stains red-brown in IKI (and is thus presumably proteinaceous or a polysaccharide).

The gradual depletion of the stained matter in the older portions of the rhizome suggests that it is a storage product.

2. **Maianthemum canadense** Desf. Ann. Mus. Natl. Hist. Nat. **9:** 54. 1807. FIGURE 7A–G, MAP 3.

Smilacina canadensis (Desf.) Pursh, Fl. Amer. Sept. **1:** 233. 1814; *Unifolium canadense* (Desf.) E. Greene, Bull. Torrey Bot. Club **15:** 287. 1888; *Maianthemum bifolium* (L.) F. W. Schmidt f. *canadense* (Desf.) Farw. Bull. Torrey Bot. Club **42:** 356. 1915. TYPE: not determined.

Smilacina canadensis (Desf.) Pursh var. *ovalis* Pursh, Fl. Amer. Sept. **1:** 233. 1814; *Unifolium bifolium* (L.) E. Greene f. *ovale* (Pursh) Farw. Bull. Torrey Bot. Club **42:** 356. 1915; *Maianthemum canadense* Desf. var. *ovale* (Pursh) Butters, Minnesota Stud. Pl. Sci. **4:** 437. 1927. TYPE: not determined.

Smilacina canadensis (Desf.) Pursh var. *trifolia* Pursh, Fl. Amer. Sept. **1:** 233. 1814; *Unifolium bifolium* (L.) E. Greene var. *trifolium* (Pursh) Farw. Bull. Torrey Bot. Club **42:** 356. 1915. TYPE: not determined.

Styrandra amplexicaulis Raf. Autik. Bot. 68. 1840. TYPE: United States, Allegheny Mtns., *Rafinesque s.n.* (holotype, PH?, probably destroyed; lectotype, here chosen, protologue).

Maianthemum canadense Desf. var. *interius* Fern. Rhodora **16:** 211. 1914; *Unifolium canadense* (Desf.) E. Greene var. *interius* (Fern.) House, Bull. New York State Mus. **254:** 224. 1924; *Maianthemum canadense* Desf. subsp. *interius* (Fern.) Löve & Löve, Bull. Torrey Bot. Club **81:** 33. 1954. TYPE: United States, South Dakota, Piedmont and Little Elk Creek, 4000 ft, 27 June 1892, *Rydberg 1043* (holotype, GH!; isotype, US!).

Maianthemum canadense Desf. var. *carolinianum* Butters, Minnesota Stud. Pl. Sci. **4:** 437. 1927. TYPE: United States, North Carolina, moist woods near Highlands, 31 May 1897, "Biltmore Herbarium" no. *16b* (holotype, MINN; isotypes, GH!, PH!, US!).

Maianthemum canadense Desf. var. *pubescens* Gates & Ehlers, Pap. Michigan Acad. Sci. **32:** 30. 1948. TYPE: United States, Michigan, Emmet or Cheboygan Co., *Gates & Ehlers s.n.* (holotype, not located; MICH?).

Maianthemum canadense Desf. f. *oswaldii* Mold. Phytologia **5:** 84. 1954. TYPE: United States, New Jersey, Bergen Co., Alpine, *Oswald s.n.* (holotype, NY).

Terrestrial forest herb, 10–25 cm tall. Roots uniform, occurring only at scale-leaf nodes, 2 to 6 per node, 8–15 cm by 0.5–1 mm. Rhizome an irregularly branched sympodium, the individual units cylindrical, 2–30 cm by 1–1.5 mm, the scale leaves 3 to 10, the internodes 0.5–5 cm long, shorter apically, the lateral buds 1 at every node, axillary, 1 to 4 forming renewal shoots; epidermis persistent; starch deposited throughout, depleted in older portions. Leafy stem upright, 10–18 cm long, 1.5–2.5 mm broad at base, the surface smooth, usually glabrous in plants of eastern North America and slightly pubescent in plants of upper Midwest; foliage leaves 2 or 3 (or 4); internodes 1.5–2.5 cm long. Upper leaf sessile, lower one(s) sessile or with petiole to 7 mm long; blade ovate to subcordate, 4.5–7(–9) by 3–4.5(–5.5) cm, the apex acute, or short-caudate (1–2 mm), the base rounded, with narrow, shallow sinus and basal lobes 2–5 mm long, the margin flat, denticles distinct, the veins ranked in strength. Inflorescence a complex raceme with 12 to 25 flowers; main axis stiff, arching upward, slightly flexuous, 3–4.5 cm long, 1–1.5 mm broad at base, round or flattened, most often smooth, green, glabrous or slightly pubescent;

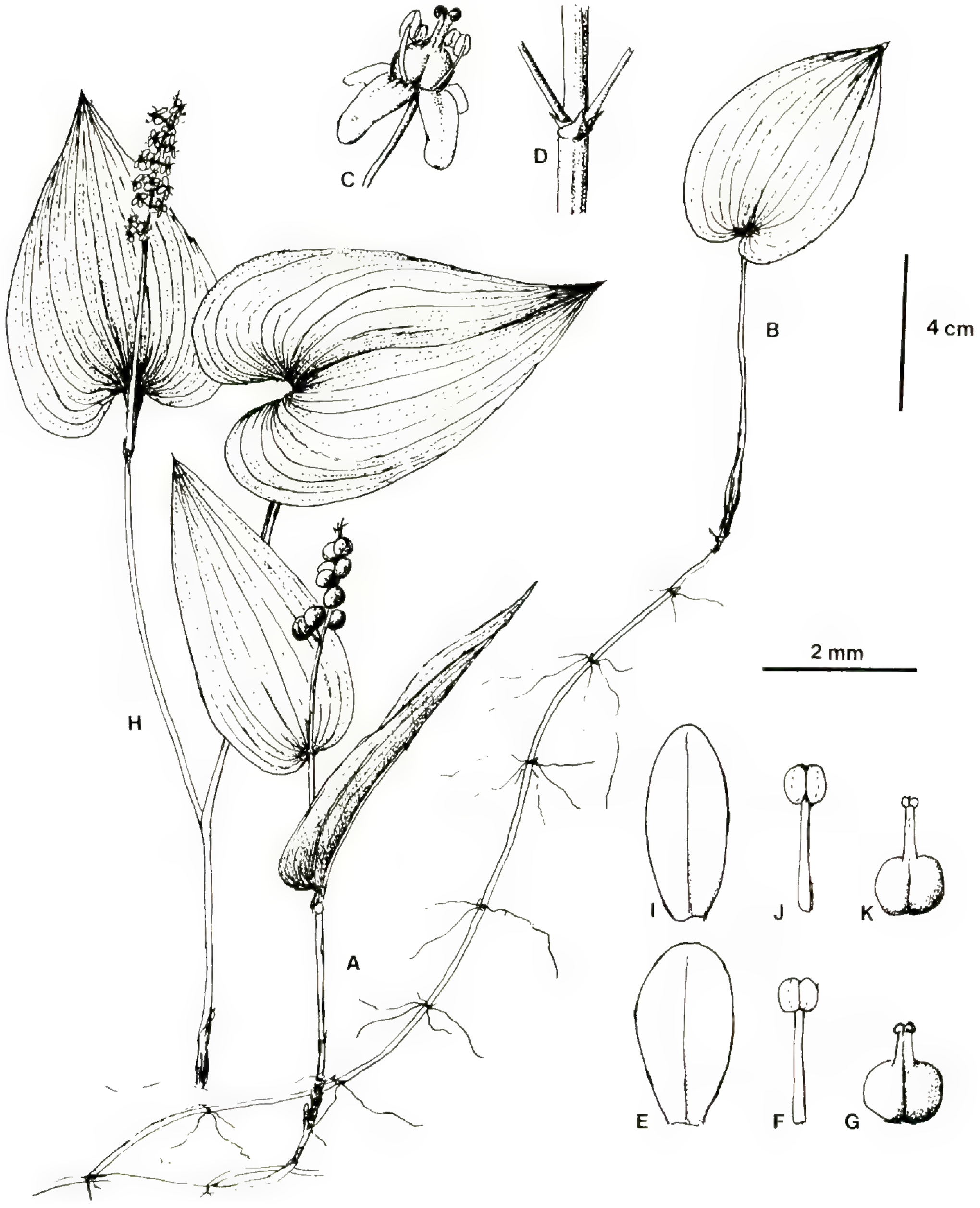
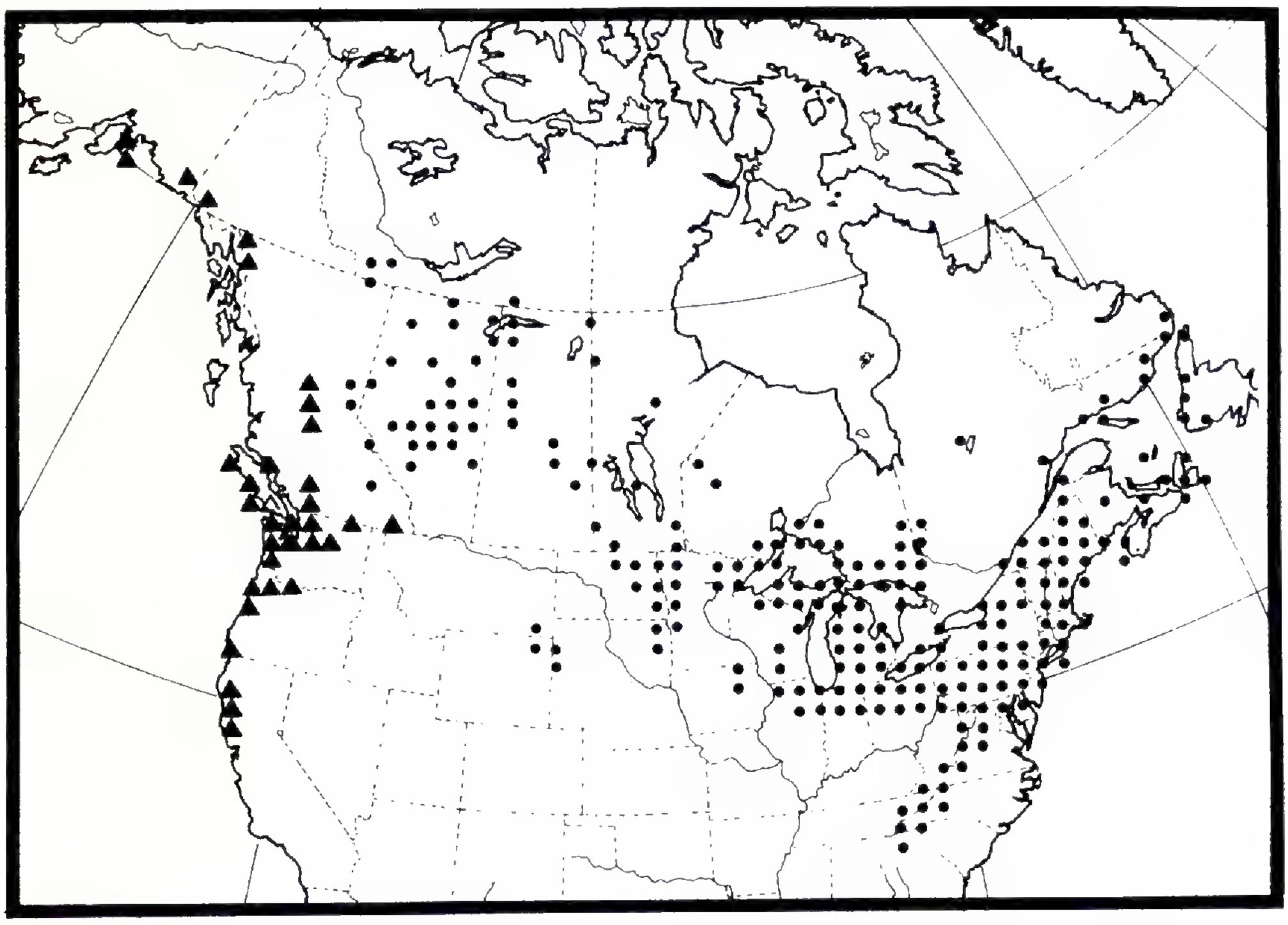


FIGURE 7. A–G, *Maianthemum canadense* (*LaFrankie 78*, GH): A, habit of bifoliate reproductive shoot; B, habit of unifoliate vegetative shoot; C, flower; D, inflorescence node with 2 pedicels, each subtended by bract, entire fascicle subtended by bract; E, tepal; F, stamen; G, gynoecium. H–K, *M. dilatatum* (*Taylor 1552*, GH): H, habit of bifoliate reproductive shoot, with long-petiolate cauline leaf; I, tepal; J, stamen; K, gynoecium.

internodes 6 to 12, 1–3 mm long; fascicles arranged in helix, with 1 to 3 (usually 2) flowers at each node, spreading, with bract subtending each fascicle. Flowers dimerous; pedicel 3–7 by 0.2–0.5 mm, ribbed, glabrous, with bract subtending; tepals uniform, weakly 2-ranked, reflexed, 1.5–2 by 0.8–1 mm, white; stamens



Map 3. Distribution of *Maianthemum canadense* (dots) and *M. dilatatum* (triangles).

inserted at tepal base, the filament 1–1.5 mm long, very thin, the anther 0.2–0.4 mm long; ovary spherical, 0.8–1 mm broad, the style 0.5–0.8 mm long, the stigma distinctly 2-lobed, 0.3–0.5 mm broad. Fruits spherical, 4–6 mm in diameter, green mottled with red when young, maturing to deep translucent red; seeds up to 2, spherical, ca. 3 mm in diameter. Chromosome number $2n = 36, 54, 72$ (Kawano, Ihara, Suzuki, & Iltis, 1967; Valentine & Hassan, 1971).

Ecology and distribution. Abundant in northern forests (nearly ubiquitous in forests of eastern Canada and the northeastern United States); sea level to 1800 m alt. Flowering May–June; fruits retained through August or September.

From Labrador (Battle Harbor, *Williamson s.n.* (GH, PH)) and Prince Edward Island (Queens Co., *Fernald 7199* (GH, PH)) south along Atlantic coast to New Jersey (Cape May Co., Cape May Courthouse, *Long 7219* (GH, PH)) and Delaware (Newcastle Co., Red Clay Creek, *Long 30211* (GH, PH)), then inland at higher elevations as far south as Virginia (Roanoke Co., McAfee Knob, *C. Wood 6055* (GH)) and North Carolina (Transylvania Co., Lake Logan, *Hardin 715* (GH)). West of Appalachians, southern limit much to north, extending across northern Indiana (LaPorte Co., W end of Hudson Lake, *Friesner 21408* (GH); and Jefferson Co. (Deam, 1940)) and Illinois (LaSalle Co., Starved Rock, *Greenman s.n.* (GH)), with outlying location in Henry Co., Missouri, *fide* Barkley (1977), although unreported there by Steyermark (1963). Northern limit extending from central Québec (Lac Mistassini, *Rousseau 2005* (GH)) through Ontario (Sandy Lake, *Moir 4065* (GH)), where nearly ubiquitous in coniferous forests although not widely collected, and to Northwest as far as Alberta (Wood

Buffalo Park, *Raup 2025* (GH)) and British Columbia (E of Bouchie Lake, *Calder 18170* (GH); 1.5 mi S of Prince George, *Calder 12341* (GH)). Western limit chiefly determined by southern and northern ones (species absent from Rockies south of Canada, despite slightly disjunct occurrence in Black Hills of South Dakota—no location, *Cutler 2623* (GH)).

The North American plants of *Maianthemum* with dimerous flowers were placed under *M. bifolium* until Desfontaines (1807) described them as the separate species *M. canadense*. I have not determined a lectotype for this species because I have not examined Desfontaines's herbarium, which was transferred to FI. A specimen of the material he studied may still be there. The specimens studied by Pursh are not at PH or any other American herbarium but may be at OXF.

The six varietal names published for this species are based on insignificant differences, and I have placed them all in synonymy. The limitation of pubescence as a varietal character is discussed under the general heading of leaf morphology. Butters (1927) claimed that the distinction between the plants of the upper Midwest and those of the East was based on vegetative features as well as pubescence. However, his data do not indicate any discrete and consistent difference between eastern and western plants; they merely demonstrate the extent to which minor vegetative differences occur within this otherwise broadly uniform species.

The three dimerous species of *Maianthemum* are very similar to one another in every important feature, and as a group, they have a continuous circumboreal distribution. Although they differ only in minor aspects of leaf shape, they have been recognized as separate species because these differences are rather constant and the species are found within relatively well-defined geographic borders. *Maianthemum canadense* is found in eastern and central North America; the upper cauline leaf is ovate to elliptic and has a very narrow basal sinus. *Maianthemum bifolium* is Eurasian in distribution; the upper cauline leaf is nearly triangular, and it has a moderately broad basal sinus. *Maianthemum dilatatum* is restricted to the Pacific coast of North America, with a limited extension to the Kamchatka peninsula and northern Japan; the upper cauline leaf is more nearly cordate, with a broad basal sinus, and the plant is nearly twice as large as that of the other two species (see FIGURE 8). In general, there is no point of sympatry or intergradation between *M. canadense* and *M. bifolium*; likewise, *M. canadense* and *M. dilatatum* are allopatric and quite distinct. However, both *M. dilatatum* and *M. bifolium* grow in eastern Asia, and considerable intergradation between the species occurs there.

The overall similarity between the three dimerous species, and the intergradation of species in eastern Asia, has led to some controversy over their proper taxonomic status. Kawano and colleagues (Kawano, Ihara, & Suzuki, 1968a, 1968b; Kawano & Suzuki, 1971; Kawano, Suzuki, & Koyima, 1971) found that the three dimerous species have a uniform karyotype, an overlapping range of morphological variation, and a relatively similar ecology but nonetheless concluded that there is ". . . reasonable certainty [the three species] are recognizable as specifically distinct entities." In light of their generally uniform vegetative and floral forms, I am inclined toward the opinion of Engler (1888)

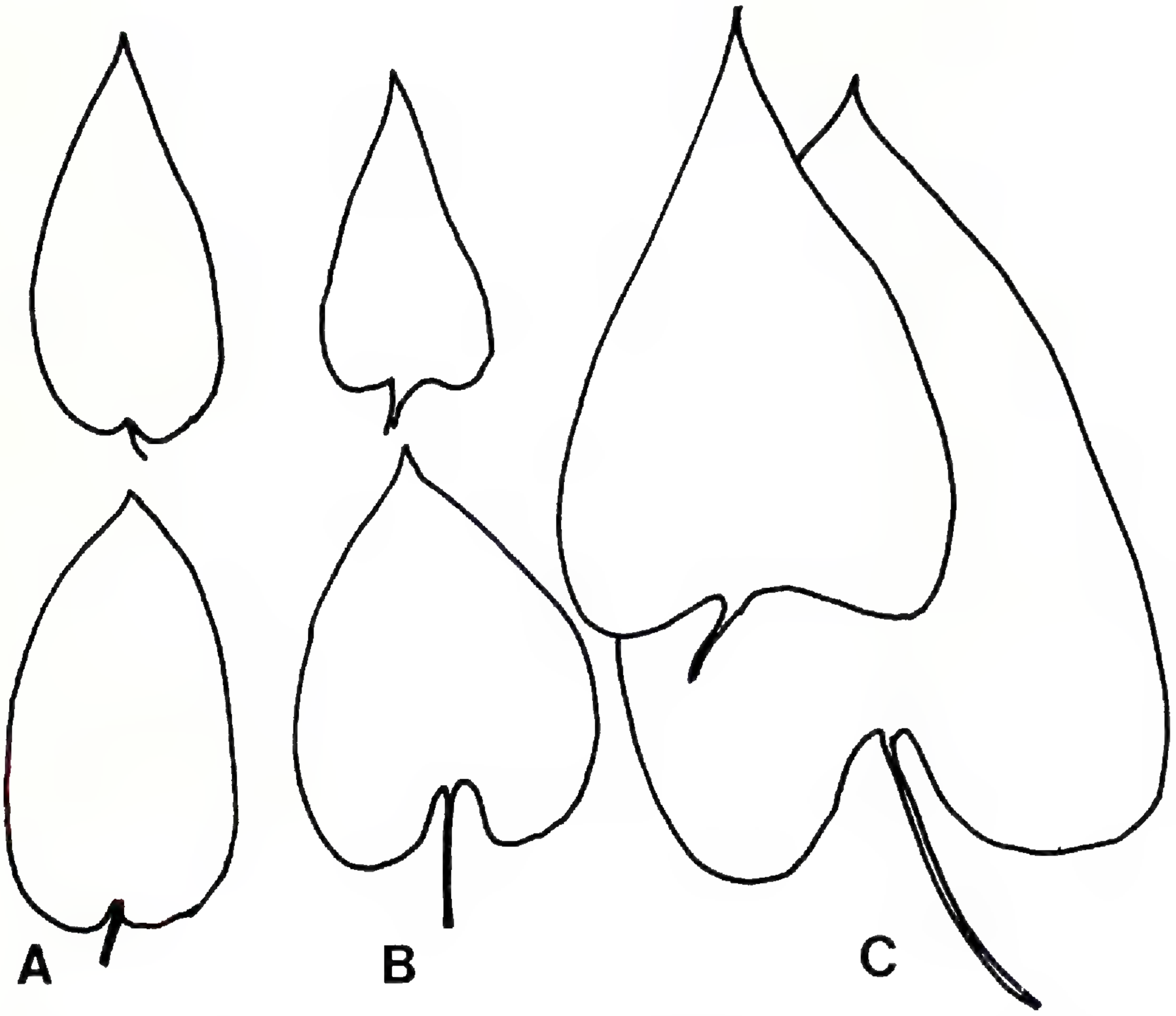


FIGURE 8. Leaf shape in 3 species of *Maianthemum* with dimerous flowers (upper cauline leaf above, lower cauline leaf below): A, *M. canadense*; B, *M. bifolium*; C, *M. dilatatum*.

and Farwell (1915) that a single species—circumboreal in distribution, and consisting of three distinct subspecies—should be recognized. However, because little is known of the interfertility of these species, and because I have not seen *Maianthemum dilatatum* or *M. bifolium* in the field, I continue to follow the conventional treatment and recognize the three species as distinct.

3. **Maianthemum dilatatum** (Alph. Wood) Nelson & Macbr. Bot. Gaz. (Crawfordsville) **61:** 30. 1916. FIGURE 7H–K, MAP 3.

Maianthemum bifolium (L.) F. W. Schmidt var. *dilatatum* Alph. Wood, Proc. Acad. Nat. Sci. Philadelphia **1868:** 174. 1868; *Smilacina dilatata* Nutt. ex Alph. Wood, *ibid.*, pro syn.; *Smilacina dilatata* Nutt. ex Baker, J. Linn. Soc., Bot. **14:** 563, 564. 1875, pro syn.; *Unifolium dilatatum* E. Greene, Man. Bot. San Francisco, 316. 1894 (with Nuttall in parentheses). TYPE: United States, [Washington,] "Columbia Woods," [ca. 1835,] *Nuttall s.n.* (lectotype, here chosen, PH!; isolectotype, GH!).

Convallaria bifolia L. var. *kamtschatica* Cham. Linnaea **6:** 587. 1831; *Smilacina bifolia* (L.) Pursh var. *kamtschatica* (Cham.) Ledeb. Fl. Ross. **4:** 127. 1853; *Maianthemum bifolium* (L.) F. W. Schmidt var. *kamtschaticum* (Cham.) Trautv. & Meyer, Fl. Ochot. **1:** 474. 1856; *Unifolium bifolium* (L.) E. Greene var. *kamtschaticum* (Cham.) Piper, Contr. U. S. Natl. Herb. **11:** 200. 1906; *Maianthemum kamtschaticum* (Cham.)

V. Komarov, Puteshestvie na Kamchatku, 451. 1909, nomen nudum, reprinted in "V. L. Komarov: Izbrannye Sochineniia" **6:** 451; *Maianthemum bifolium* var. *kamtschaticum* (Cham.) Jepson, Fl. W. Calif. 109. 1911; *Unifolium kamtschaticum* (Cham.) Gorman, Muhlenbergia **2:** 376. 1916; *Maianthemum kamtschaticum* (Cham.) Nakai, Bot. Mag. (Tokyo) **31:** 282. 1917; *Maianthemum canadense* Desf. var. *kamtschaticum* (Cham.) Kudo, J. Coll. Agric. Tohoku Imp. Univ. **11:** 92. 1922; *Maianthemum dilatatum* (Alph. Wood) Nelson & Macbr. var. *kamtschaticum* (Cham.) Butters, Minnesota Stud. Pl. Sci. **1:** 443. 1927; *Maianthemum bifolium* subsp. *kamtschaticum* (Cham.) E. Murray, Kalmia **12:** 22. 1982. TYPE: U.S.S.R., Kamchatka peninsula (no specimen cited, probably at LE).

Maianthemum intermedium Vorosch. Bjull. Glavn. Bot. Sada **38:** 50. 1960. TYPE: U.S.S.R., Regio Primorsky, Vladivostok, prope Okeanskaja, in sylvis, 7 Sept. 1950, *Woroschilov s.n.* (MHA).

Terrestrial forest herb, to 45 cm tall. Roots uniform, occurring only at scale-leaf nodes, 2 to 6 per node, 8–20 cm by ca. 1 mm. Rhizome an irregularly branched sympodium, the individual units cylindrical, 10–20 cm by 1.5–2.5 mm, the scale leaves 3 to 10, the internodes 1.5–3 cm long, shorter apically, the lateral buds 1 at every node, axillary, 1 to 4 developing as leafy shoots; epidermis persistent; carbohydrate reserves not known. Leafy stem upright, 15–35 cm long, 2–4 mm broad at base, the surface smooth, glabrous; foliage leaves 2 or 3 (or 4); internodes 4–8 cm long. Upper leaf subpetiolate, lower one with petiole (2.7–)4–7(–8) cm long; blade cordate, 6–10 by 5–8 cm, the apex sharply acute, the base lobed, with very deep sinus and lobes 2.5–3.5 cm long, the margin flat, denticles indistinct, the veins ranked. Inflorescence a complex raceme with 15 to 40 flowers; main axis arching upward, slightly flexuous, 3.5–5 cm long, 0.8–1.5 mm broad at base, rounded or flattened, weakly ribbed, green, glabrous; internodes 10 to 18, 1–3 mm long; fascicles arranged in helix, with 1 to 4 (or 5) flowers at each node, spreading, bract subtending each fascicle. Flowers dimerous; pedicel 3–5 by 0.2–0.4 mm, ribbed, glabrous, with bract subtending; tepals uniform, reflexed, 2–3.2 by ca. 1.5 mm, white; stamens inserted at tepal base, the filament 1.5 mm long, very thin, the anther 0.2–0.3 mm long; style 0.4–0.5 mm long, stigma distinctly 2-lobed. Fruits spherical, 4–6 mm in diameter, green with red spots when young, maturing to translucent red; seeds 1 or 2, spherical, 2–3 mm in diameter. Chromosome number $2n = 36$ (Kawano, Ihara, Suzuki, & Iltis, 1967; Kawano & Suzuki, 1971).

ECOLOGY AND DISTRIBUTION. Forming dense patches on floor of coniferous and deciduous forests, most abundant in light gaps and near forest margins; broad ecological latitude with respect to light and soil type (Kawano, Ihara, & Suzuki, 1968a, 1968b); sea level to 800 m alt. Flowering May–June; fruits ripening slowly, retained through September or October.

Species generally of Pacific coast of Northwest, ranging eastward to northern Idaho (Bonner Co., Priest Lake, *Piper 3685* (GH)) and southward to northern California (Humboldt Co., Bishop Pine Lodge, Trinidad, *Parks 4289* (GH)). Rather common along Canadian coast as far north as northern British Columbia (Haines Road, Mile 45, *Taylor 1552* (GH); Queen Charlotte Island, *Dawson s.n.* (GH)); less common along northern Pacific through Alaska (Attu Is., *Wil-*

liams 3180 (GH)), and again relatively more common in Kamchatka and northern Japan.

The name of this species is somewhat controversial. Ingram (1966) claimed that Greene's publication of *Unifolium dilatatum* was independent of Wood's earlier publication of *Maianthemum bifolium* var. *dilatatum,* and since there were no holotypes, he felt that the two names should be lectotypified by different specimens. This is important because Nelson and Macbride based their binomial on Wood's, not on Greene's, epithet. As Ingram noted, if the names of Greene and Wood have different types, then the publication of *M. dilatatum* based on Greene is still necessary, yet would create a later homonym that would, in effect, make *M. kamtschaticum* the correct binomial. However, contrary to Ingram's opinion, there is no reason to believe that the names should be lectotypified by different specimens. Greene was an authority on botanical literature, especially with regard to plants of the western United States, and therefore would surely have been aware of Wood's use of Nuttall's name as a varietal epithet. The fact that Greene chose to place Nuttall's rather than Wood's name in parentheses simply reflects his desire to use the earliest reference for every name. Greene's name is best viewed as simply a new combination in a new ranking of Wood's, and it therefore automatically has the same type as the earlier epithet; in consequence, there is no reason to change the name from the one in common use. The Nuttall specimen from "Columbia Woods" in PH is probably the specimen seen by Wood, or if not, it is a duplicate. In either case it should be the lectotype, not the neotype, as determined by Ingram (1966).

4. **Maianthemum flexuosum** (Bertol.) LaFrankie, Taxon **35:** 588. 1986.
FIGURE 9, MAP 4.

Smilacina flexuosa Bertol. Nov. Comment. Acad. Sci. Inst. Bononiensis **4:** 411. *t. 4.* 1840 (not Fl. Guatimal. 1840); *Smilacina bertolonii* Kunth, Enum. Pl. **5:** 151. 1850, nomen illegit.; *Tovaria flexuosa* (Bertol.) Baker, J. Linn. Soc., Bot. **14:** 567. 1876; *Vagnera flexuosa* (Bertol.) Standley, J. Wash. Acad. Sci. **15:** 457. 1925. TYPE: Guatemala, ca. 1830, *Velasquez s.n.* (holotype, BOLO, IDC 748. 45: II. 5!).

Smilacina flexuosa Hooker, Icon. Pl. n.s. **2:** *t. 529.* 1843, non Bertol. 1840. TYPE: Guatemala, ca. 1830, *Skinner s.n.* (holotype, K!).

Smilacina flexuosa Bertol. var. *erubescens* Emons, Ann. Missouri Bot. Gard. **32:** 405. 1945. TYPE: Guatemala, San Marcos, between Todos Santos and Finca El Porvenir, 1300–3000 m, 1 March 1940, *Steyermark 36972* (holotype, F!).

Terrestrial forest herb, 0.40–0.75 m tall. Roots uniform, 10 to 18 per rhizome unit, scattered but most numerous at base of leafy shoot, 20–35 cm by 1–1.5 mm. Rhizome a linear sympodium, occasionally forking, the individual units 2–4(–7) by 1–2 cm, slightly flattened, the scale leaves 7 or 8, the internodes 5–8(–20) mm long, shorter apically, the lateral buds 6 or 7, axillary, 1 or 2 developing as leafy shoots; epidermis replaced by periderm; starch deposited in distal portions. Leafy stem arched, 40–70 cm long, 3–4 mm broad at base, the surface slightly ribbed, glabrous; foliage leaves 7 to 9 (to 12); internodes 3.5–6(–10) cm long, shorter apically. Leaves with petiole less than 5 mm long; blade ovate to lanceolate, 8–12 by 3–5 cm, the apex long-acuminate (upper

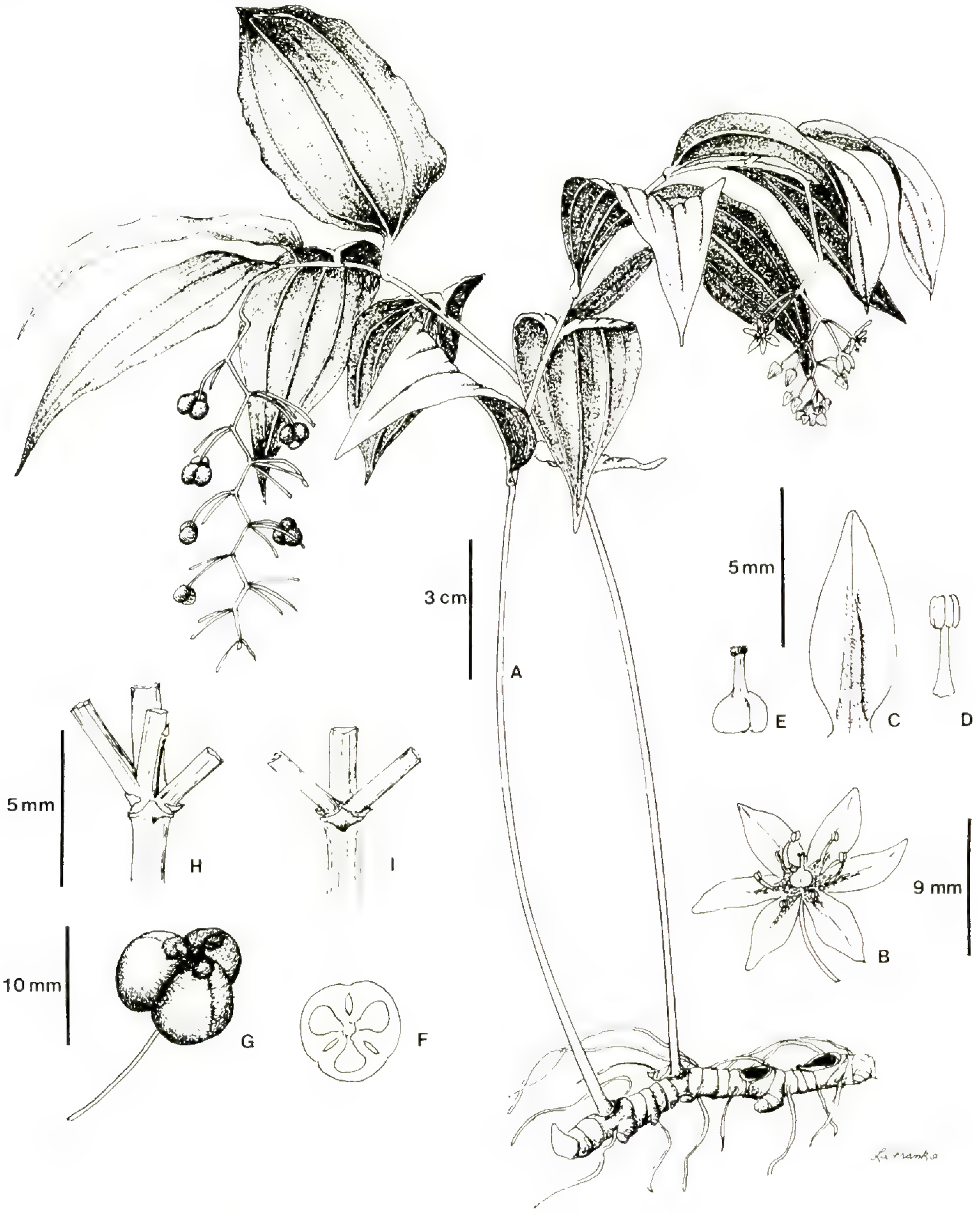
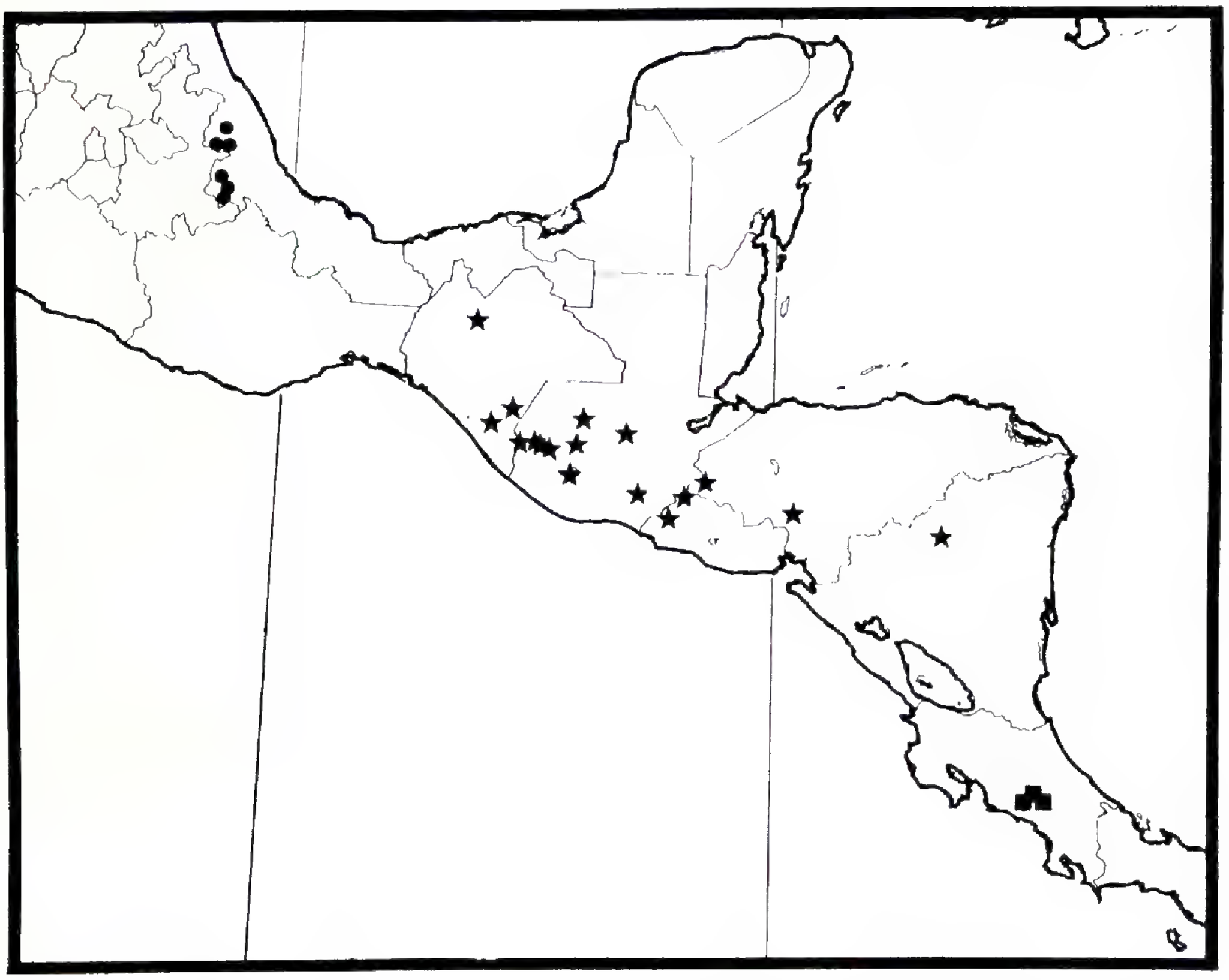


FIGURE 9. *Maianthemum flexuosum* (*LaFrankie 84-V-22A*, GH): A, rhizome, leafy shoot, both fruit and flowers on same individual; B, flower; C, tepal; D, stamen; E, gynoecium; F, ovary, transverse section, showing 3 locules, 3 cavities of septal nectaries; G, mature fruit; H, I, lateral fascicles.

leaves) or acute to short-acuminate (lower ones), the base rounded to slightly tapered, the margin undulating, entire or rarely denticulate, the veins ranked, the surfaces glabrous, rarely with minute hairs. Inflorescence a complex raceme with 25 to 65 flowers; main axis pendent, flexuous, tapering, 5–18 cm long, 1.5–3 mm broad at base, smooth or slightly ribbed, green, glabrous; internodes 10 to 16, 6–8(–20) mm long; fascicles distichous, with 2 to 4 (to 6) flowers, slightly reflexed and drooping, bract subtending each fascicle. Flowers trimer-



MAP 4. Distribution of *Maianthemum flexuosum* (stars), *M. macrophyllum* (dots), and *M. paludicolum* (squares).

ous; pedicel 8–21(–28) by 0.4–0.6 mm, slightly ribbed, glabrous, with bract subtending (sometimes central pedicel of fascicle with additional bract at mid-length); tepals uniform, spreading to reflexed, 5–11 by 2–3 mm, lavender to pink, rarely white or green-white; stamens epitepalous, 0.5–1 mm above tepal base, the filament narrow-petaloid, 1.5–3 mm long, the anther 0.5–1(–1.5) mm long; ovary spherical to cylindrical, 1 by 1.5–2 mm, the style 1–2 mm long, the stigma 3-lobed, ca. 0.5 mm broad. Fruits distinctly 3-lobed, 7–11 mm broad, green when young, maturing to red; seeds 1 to 3, spherical, 5–6 mm in diameter. Chromosome number not known.

ECOLOGY AND DISTRIBUTION. Solitary or weakly clonal, in understory of cloud forests; 1450–2200(–2800) m alt. Flowering January–June; fruits set May–August, retained August through following spring; fruiting and flowering stems sometimes overlapping on same individual.

Northwestern limit represented by single specimen from northern highlands of Chiapas, but this location recently cleared. Most common in Sierra Madre del Sur from Chiapas through Guatemala, ranging east to El Salvador; also on scattered mountains in Honduras and Nicaragua.

SPECIMENS EXAMINED. **Mexico.** CHIAPAS: vic. Pueblo Nuevo Solistahuacán, *Harrell 438* (MEXU); Naquivil, vic. Motozintla, *Breedlove 42749* (DS); Mt. Ovanda, *Matuda 374* (MEXU, MICH); vic. Escuintla, *Matuda 4237* (F, GH, LL, MEXU, MO, NY, US); Siltepec, *Matuda 15266* (DS, F, MEXU); Saxchanal, *Matuda 17808* (F, MEXU); Chicarras, *E. Nelson 3762*

(US); Cerro del Boquerón, *Purpus 7415*; vic. Volcán Tacaná, *Breedlove 31634* (DS), *Matuda 2846* (F, GH, LL, MEXU, MO, US). **Guatemala.** HUEHUETENANGO: Concepción near San Martín, *Seler 3168* (GH, US); Cerro Pixpix, Ixtahuacán, *Steyermark 50561* (F). QUICHÉ: Nebaj, *Heyde 4647* (GH, K, US). ALTA VERAPAZ: vic. Tactic, *Standley 90345* (F), *L. O. Williams 40595* (F, MICH). SAN MARCOS: Volcán Tajumulco, *L. O. Williams 26881* (F, NY, US); Barranca Eminencia, *Standley 86507* (F). QUEZALTENANGO: Cantón La Esperanza, 6 km from San Juan Ostuncalco, *Molina 16647* (F, NY); vic. Volcán Zunil, *Standley 86027* (F), *L. O. Williams 22984* (F, NY); above Santa María de Jesús, *Standley 84859* (F). TOTONICAPÁN: Cerro María Tecúm, *L. O. Williams 23119* (F). SOLOLÁ: Volcán Santa Clara, *Steyermark 46885* (F); Volcán San Pedro, *Steyermark 47227* (F); Volcán Atitlán, *Steyermark 47382* (F). SUCHITEPÉQUEZ: Volcán Agua, *Kellerman 7295* (F, NY, US); Volcán Santa Clara, *Steyermark 46722* (F, NY). CHIMALTENANGO: San Martín, *J. R. Johnston 1305* (F); Chichavac, *Skutch 72* (US); Cerro Tecpán, *Standley 58708* (F); Los Positos above Las Calderas, *Standley 58708* (F). ESCUINTLA: Volcán Agua, *Almeda 758* (DUKE), *Utley 56* (DUKE), *R. L. Wilbur 14754* (DUKE). JALAPA: Volcán Jumay, *Steyermark 32400* (F). SANTA ROSA: Santa Rosa, *Heyde 3537* (GH, K, NY, US); Zamorora, *Heyde 4652* (GH, NY, US). ZACAPA: between Loma el Picacho and Cerro de Monos, *Steyermark 42780* (F, NY). **El Salvador.** SANTA ANA: Montecristo, *Molina 12522* (F, NY). **Honduras.** INTIBUCÁ: Slone Ardisia, *Molina 6369* (F, LL). LA PAZ: Sierra Guajiquiro, 5 km from Sabaneta, *Molina 13896* (F, LL, NY, US). **Nicaragua.** MATAGALPA: Cordillera Dariense, Hacienda Santa María de Ostuma, *Tomlin 129* (MO); summit of Cerro El Picacho, *D. Stevens 22166* (MO).

The type specimen of *Maianthemum flexuosum* was recently discovered in BOLO, together with many other Guatemalan types of Bertoloni. Duncan (1983) presented a concise history of the Guatemalan specimens upon which the *Florula Guatimalensis* was based but erroneously concluded that the material had been destroyed during the Second World War. Evidently the specimens were simply misplaced, perhaps after being photographed by IDC for their microfiche edition of the Bertoloni Herbarium. A revised history of the Bertoloni material is now being prepared by the staff at BOLO.

This species is sometimes confused with *Maianthemum scilloideum,* the only other terrestrial species of Central America with a racemose inflorescence, although in their typical forms these species are thoroughly distinct. They are readily distinguished from one another by quantitative differences of the inflorescence (see TABLE) and also by differences in rhizome, floral morphology, and habitat. *Maianthemum scilloideum* is a spreading, clonal herb of high altitudes, typically found in coniferous forests above 2500 m, while *M. flexuosum* is often solitary and is a plant of wet, broad-leaf cloud forests below 2500 m. The rhizome of *M. flexuosum* is broader, less elongate, and more densely packed with starch, especially in the distal portions. The inflorescence of *M. flexuosum* is pendent rather than upright and is at least slightly flexuous, the tepals are usually tinted with lavender, and the stamens are generally inserted 1 mm or so above the tepal bases.

5. **Maianthemum gigas** (Woodson) LaFrankie, comb. nov.

Smilacina gigas Woodson, Ann. Missouri Bot. Gard. **27**: 270. 1940. TYPE: Panama, Chiriquí, trail from Cerro Punta to headwaters of Río Caldera, 2250–2500 m, 14 Jan. 1939, *P. Allen 1446* (holotype, MO!; isotype, GH!).

Terrestrial or sometimes epiphytic herb, 0.8–2.5 m tall. Roots uniform, 10 to 15 per rhizome unit, evenly scattered, 30–60 cm by 2–4 mm. Rhizome a

Morphometric comparison of inflorescences of Maianthemum scilloideum and M. flexuosum.*

Character	*M. scilloideum* Range	Median	Mean	*M. flexuosum* Range	Median	Mean
Inflorescence length (cm)	1.6–8.3	2.9	2.9 ± 0.9	5–18	9.1	10.4 ± 1.4
Flowers per inflorescence	4 to 27	15	15.5 ± 2.5	8 to 65	30	34.8 ± 5.6
Flowers per fascicle	1 to 3	3	2.5 ± 0.2	2 to 6	3	3.2 ± 0.3
Pedicel length (mm)	3–4.5	4	4.2 ± 0.5	8–21	14.5	14.5 ± 1.4

*Results expressed as range, median, and mean with 95% confidence interval.

massive, forking sympodium, the individual units broad-claviform to subspherical, 3–4 cm broad, the scale leaves 8 or 9, the internodes 2–5 mm long, the lateral buds 6 or 7, axillary, 1 or 2 developing as leafy shoots; epidermis replaced by periderm; starch only near rhizome apex. Leafy stem leaning or arching, 75–250 cm long, 8–15 mm broad at base, the surface smooth, glabrous; foliage leaves 10 to 16; internodes 3–5.5 cm long. Leaves with petiole 4–5 mm long; blade ovate to elliptic, 14–30(–38) by 5–9(–11) cm, the apex acuminate, the base tapered or rounded, the margin undulating, denticles distinct but very small, the veins ranked, the surfaces glabrous. Inflorescence a pyramidal panicle with 45 to 400 flowers; main axis arching upward, straight, stiff, 15–29 cm long, 2.5–4 mm broad at base, ribbed, light green-white, or red-purple, glabrous; internodes 25 to 30, most 2–15 mm long; lateral branches racemose, arranged in helix, spreading or slightly ascending, 6–15 cm long, with 1 or 2 flowers at base and others inserted at 1–4(–10) mm intervals, bract subtending each lateral raceme. Flowers trimerous; pedicel 2–5(–7) by 0.5–0.8 mm, deeply ribbed, glabrous, with bract subtending; tepals uniform, spreading, (2.5–)3–5 by 1.3–2.3 mm, white, sometimes with purple spots; stamens inserted at tepal base, the filament 2–3.5 mm long, thin, the anther oblong, 0.5–1 mm long; ovary spherical to cylindrical, 1–1.5 mm in diameter, the style 0.8–1.2 mm long, the stigma 3-lobed, 0.7–1 mm broad. Fruits spherical to weakly 3-lobed, 10–12 mm broad, green mottled with red when young, maturing to red; seeds up to 6, usually spherical, 4–6 mm in diameter. Chromosome number $2n = 36$ (Kawano & Iltis, 1966).

The Central American species of *Maianthemum* with paniculate inflorescences are often difficult to identify from herbarium material alone, which is perhaps why previous taxonomic treatments of this group have lumped all such specimens under "*M. paniculatum*." The flowers are relatively uniform when dried, and the species differ chiefly in the shape of the rhizome, the number of foliage leaves, and the form of the inflorescence. The rhizome and the foliage leaves are often missing from herbarium specimens, and the question of inflorescence morphology is often confounded by uncertainty as to the plant's level of maturity. A rule of thumb helpful in determining maturity is that a plant is full size when the length of the inflorescence exceeds that of the pen-

ultimate foliage leaf. Despite this information, many immature shoots within the paniculate group cannot be adequately identified.

I have recognized four species (*Maianthemum paniculatum, M. gigas, M. paludicolum, M. septifolium*) and two varieties bearing paniculate inflorescences. The species can be identified by several vegetative features, and although I suspect that floral differences are also present, they are not easily observed in dry material. Potentially useful floral features include shape of the ovary, morphology of the septal nectary and pore, number of ovules, and color of immature fruit. The present treatment of the paniculate group is an improvement over the aggregation of all types within a single species, but it remains unsatisfactory in its failure to identify decisive floral differences between species. The plants of western Panama are especially diverse. Woodson and Schery (1940) determined that the very large plants of Panama were a new species (*M. gigas*) and were clearly distinct from the smaller and more widespread plants, which they took to be *M. paniculatum.* Later, Woodson and Schery (1945) reduced *M. gigas* to the synonymy of the latter species. My study of this group throughout Meso-America indicates that Woodson was originally correct in his analysis, but I was unable to determine any consistent difference in floral morphology between the two species. Further study on this point should be directed toward western Panama, where they both occur, and field study of floral morphology should be emphasized.

As mentioned, there are many singular collections that fall within the range of *Maianthemum gigas,* but I recognize only the previously described taxon *M. gigas* var. *crassipes* as distinct, and I would suggest that any new varieties in this species be based on field study rather than on herbarium specimens alone.

Key to the Varieties of *Maianthemum gigas*

Tepals 5–7 by 3–3.5 mm, yellow or yellow-white; perianth cupuliform; pedicel 0.8–1 mm broad. ..... 5a. var. *crassipes.*

Tepals 2.5–5 by 1.5–2 mm, white or white infused with lavender; perianth spreading; pedicel 0.4–0.7 mm broad. ..... 5b. var. *gigas.*

5a. **Maianthemum gigas** var. **crassipes** (Standley & Steyerm.) LaFrankie, comb. et stat. nov.

FIGURE 10A–G, MAP 5.

Smilacina crassipes Standley & Steyerm. Publ. Field Mus. Nat. Hist., Bot. Ser. **23:** 214, 215. 1947. TYPE: Guatemala, Huehuetenango, Cerro Pueblo Viejo, rocky slope above La Libertad, 1900 m, 20 Aug. 1942, *Steyermark 51003* (holotype, F (F no. *1129142*!); isotype, F!).

Terrestrial or epiphytic herb, 0.7–1.3 m tall. Roots not seen. Rhizome not seen. Leafy stem arching or pendent, 70–130 cm long, glabrous. Leaves with petiole 2–4 mm long. Inflorescence a diffusely flowered pyramidal panicle with 40 to 130 flowers; main axis straight, stiff, tapering, 10–15 cm long, 3–4 mm wide at base, deeply ribbed, green, glabrous; internodes 25 to 30, most 2–6 mm long; lateral axes with 5 to 7 flowers. Flowers with pedicel 5–8 by 0.8–1 mm, deeply ribbed, glabrous; perianth suberect or cupuliform at anthesis; tepals 7–9 by 3–3.5 mm, pale yellow; stamens with filament 3–5 mm long, thin,

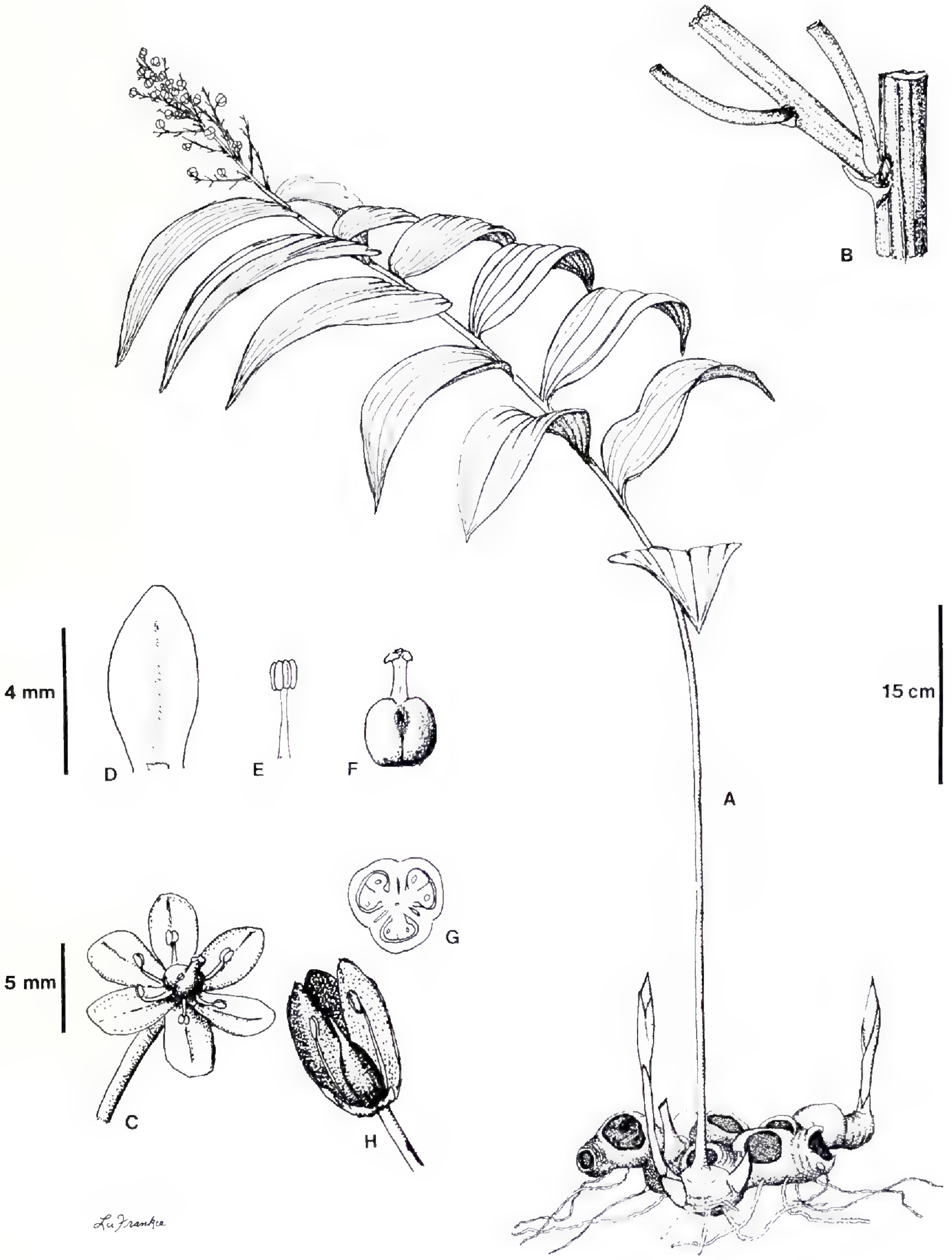
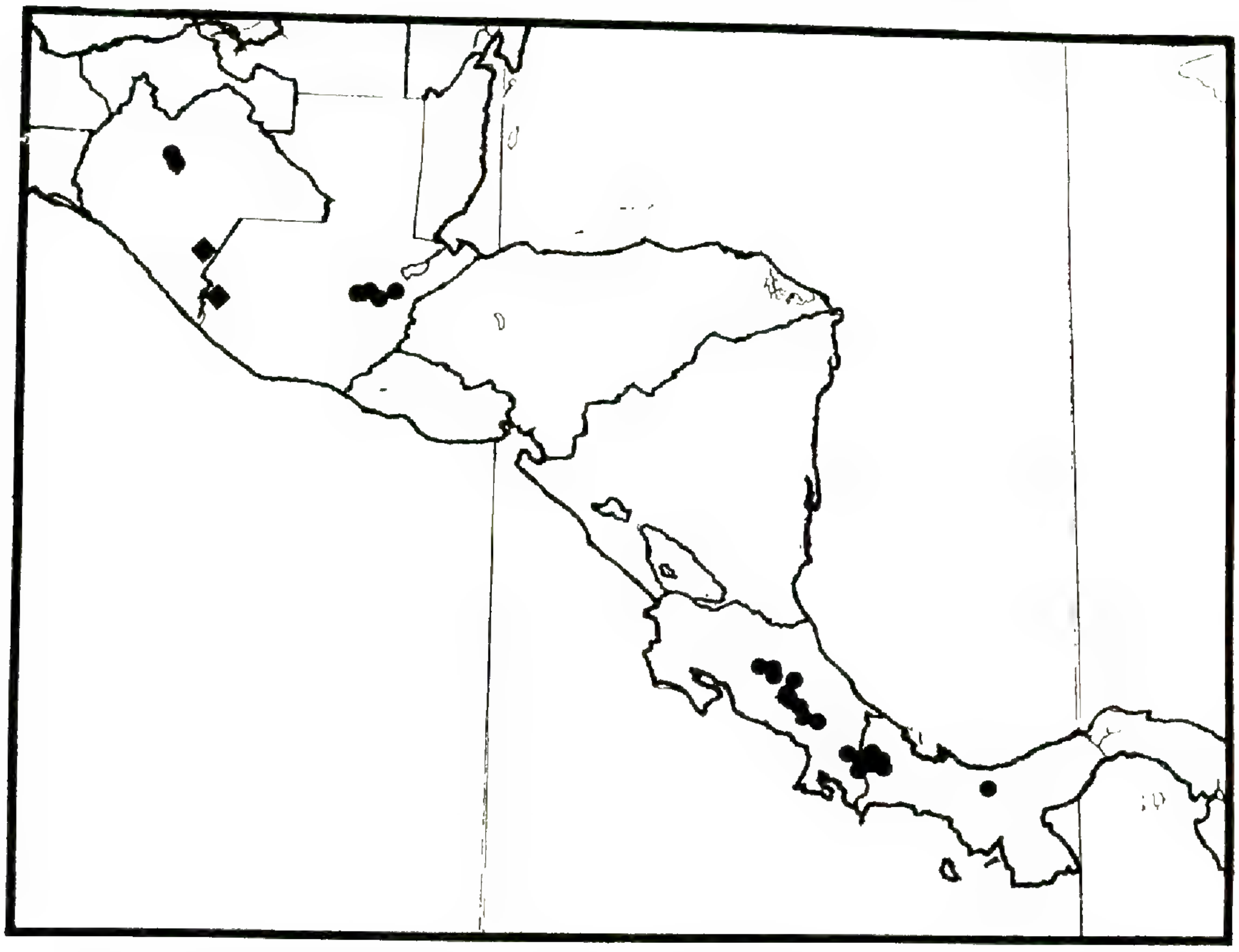


FIGURE 10. *Maianthemum gigas*. A–G, var. *gigas* (*LaFrankie 83-IV-10A*, GH): A, rhizome, leafy shoot, and infructescence; B, detail of lateral raceme of infructescence; C, flower; D, tepal; E, stamen; F, gynoecium; G, ovary, transverse section, showing 6 ovules, 3 cavities of septal nectaries. H, var. *crassipes* (*Matuda 4702*, LL), flower.

anther 1.2–1.6 mm long; ovary cylindrical, 2.5–3 by 1.5–2 mm, the style 1.5–2.4 mm long, the stigma 3-lobed, as broad as style. Fruits spherical, 8 mm in diameter, red when mature; seeds 1 to 6, oblong-cuneate, 2.5–3.5 mm long. Chromosome number not known.



MAP 5. Distribution of *Maianthemum gigas*: var. *gigas* (dots) and var. *crassipes* (diamonds).

ECOLOGY AND DISTRIBUTION. Very rare (known from three collections only); described once as an epiphyte, twice as terrestrial ("on rocks"?) at 1900 m alt.

Guatemala, and Chiapas, Mexico.

SPECIMENS EXAMINED. **Mexico.** CHIAPAS: Mt. Malé, near Porvenir, [Arroyo?] Potrero, 3200 m, *Matuda 4702* (LL, MO). **Guatemala.** SAN MARCOS: Finca El Porvenir, Potrero Tojo, Volcán Tajumulco, 1300–1350 m, *Steyermark 37655* (F).

Maianthemum gigas var. *crassipes* is a very rare and little-known taxon. It is similar to other large, paniculate species of Central America, and because of its large leaves and flowers I align it with *M. gigas* (see further discussion of the paniculate species and varieties under the species heading).

5b. **Maianthemum gigas** var. **gigas** FIGURE 10H, MAP 5.

Terrestrial or sometimes epiphytic herbs, 0.8–2.5 m tall. Leafy stem leaning or arching, 75–250 cm long, 8–15 mm broad at base, the surface smooth, glabrous. Leaves with petiole 4–5 mm long. Inflorescence a dense pyramidal panicle with 50 to 400 flowers; main axis arching upward, stiff, 15–29 cm long, 2.5–4 mm wide at base, ribbed, light green-white, or red-purple, glabrous; lateral axes with 10 to 20 flowers. Flowers with pedicel 2–5(–7) by 0.4–0.7 mm, deeply ribbed, glabrous; tepals uniform, spreading, (2.5–)3–5 by 1.3–2.3 mm, white, sometimes with purple spots; stamens inserted at tepal base, the

filament 2–3.5 mm long, thin, the anther subspherical, 0.5–1 mm broad; ovary spherical to cylindrical, 1–1.5 by 1–1.5 mm, the style 0.8–1.2 mm long, the stigma 3-lobed, 0.7–1 mm broad. Fruits spherical to weakly 3-lobed, 8–10 mm broad, green mottled with red when young, maturing to red; seeds up to 6, usually spherical, 4–6 mm in diameter. Chromosome number $2n = 36$ (Kawano & Iltis, 1966).

ECOLOGY AND DISTRIBUTION. Widespread, with broad ecological range. Most often terrestrial along roadsides, in secondary vegetation or openings, sometimes persisting in shade; also epiphytic to height of several meters. Flowering and fruiting throughout year, but less commonly January–March.

Widely distributed throughout most of Meso-America; rare in Chiapas, scattered in Guatemala (in Sierra Madre del Sur and Sierra Las Minas), common above 2000 m alt. in Costa Rica and western Panama.

SPECIMENS EXAMINED. **Mexico.** CHIAPAS: Pueblo Nuevo Solistahuacán, *Tillet 636-20* (US). **Guatemala.** ALTA VERAPAZ: road to Finca Sepacuité, 3850–4000 ft, *Luteyn 3538* (DUKE). **Costa Rica.** HEREDIA: between San Rafael and Río Las Vueltas, *D. Stevens 13930* (MO); Volcán Barba, *Utley 2313* (F), *Wilbur 17058* (DUKE, F). SAN JOSÉ: between Canaan and Chirripó, above Río Talari, *Burger 7414* (F), *8321* (F). CARTAGO: Volcán Irazú, *Allen 690* (F, GH), *Lems 650129* (NY), *Rodriguez 175* (UC), *Seibert 1636* (MO), *Stork C463* (UC, US); Volcán de Turrialba, *Standley 35186* (F); 10 km S of Hacienda Tapanti, *Burger 5648* (F); Parque Nacional Chirripó, *Davidse 24838* (MO); San Rafael de Oreamuno, *Echeverria 469* (F). LIMÓN: Cerro Kámuk, *Davidse 26009* (MO). **Panama.** BOCAS DEL TORO: headwaters of Río Culubre, *Davidse 25204* (MO). CHIRIQUÍ: vic. Cerro Punta, *Croat 48624* (MO), *Luteyn 3810* (DUKE), *4623* (DUKE), *4626* (DUKE), *Mori 5657* (MO), *7239* (MO), *Sytsma 2081* (MO), *Wilbur 13204* (F, GH, LL, MICH, MO, NY), *24218* (DUKE), *24253* (DUKE); Palo Alto, E of Boquete, *Stern 1062* (GH, MO, UC, US); above Boquete, *Croat 15754* (DUKE), *Lewis 559* (MO); Cerro Pato de Macho, 5 mi NE of Boquete, *Antonio 2676* (MO), *D'Arcy 12635* (MO); Cerro Colorado, *Antonio 1408* (MO), *Folsom 1772* (MO); vic. Bajo Mona and Quebrada Chiriquí, *Woodson 512* (GH, MO, NY); Bajo Chorro, *Davidson 53* (F, GH, MO, US); Cerro Respinga, *Gentry 5913* (MO); Cerro Horqueta, *Hagar 2017* (MO). VERAGUAS: N of Santa Fe, Cerro Arizona, *Hammel 4712* (MO); vic. Santa Fe, trail to Cerro Tute, *Antonio 1979* (MO).

6. **Maianthemum macrophyllum** (M. Martens & Galeotti) LaFrankie, Taxon **35:** 588. 1986. FIGURE 11, MAP 4.

Smilacina macrophylla M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles **9:** 387. 1842. TYPE: Mexico, Veracruz, on oaks near Jalapa and Totutla, 3000–4000 ft, 1840, *Galeotti 5473* (lectotype, here chosen, BR (BR no. *3394/84-2*!); isolectotype, BR (BR no. *3394/84-3*!)).

Epiphytic herb, 0.75–1.25 m tall. Roots uniform, fewer than 15 per rhizome unit, evenly scattered, length not known, 1–2 mm broad. Rhizome a forking sympodium, the individual units subspherical, 4–7 cm broad, the number of scale leaves not known, the internodes uniform, 2–5 mm long, the lateral buds at most internodes, axillary; epidermis replaced by periderm; carbohydrate reserves not known. Leafy stem slightly arching, 75–120 cm long, 5–9 mm broad at base, glabrous, polished; foliage leaves 13 to 18; internodes 2.5–4 cm long, shorter apically. Leaves with petiole 5–9 mm long; blade ovate to lanceolate, upper ones 14–21 by 4.5–8 cm, lower ones 10–16 by 5–8 cm, the apex

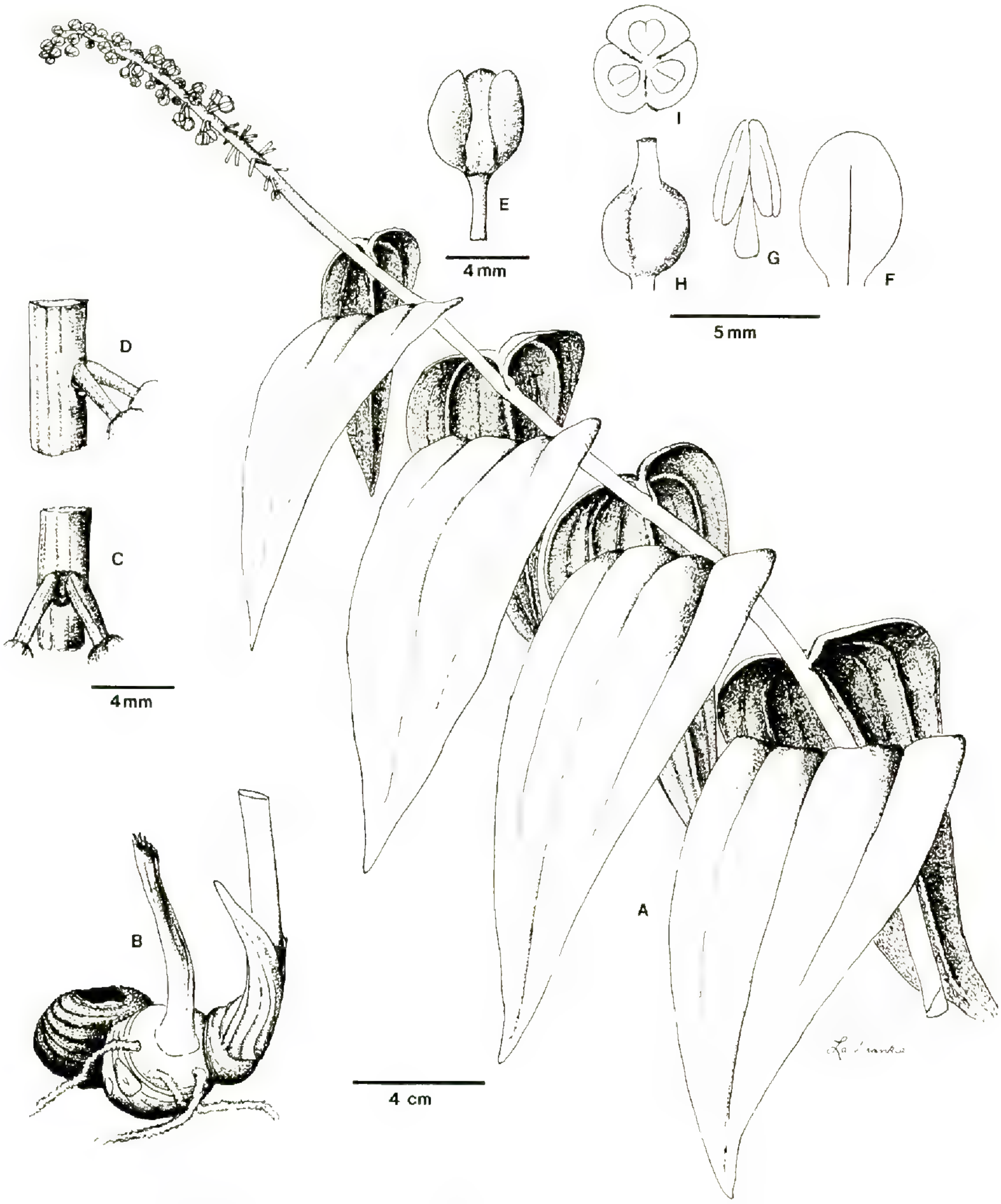


FIGURE 11. *Maianthemum macrophyllum* (*LaFrankie 84-V-11A*, GH): A, upper portion of leafy shoot and inflorescence; B, rhizome; C, D, lateral fascicles; E, flower at anthesis; F, tepal; G, stamen; H, gynoecium; I, ovary, transverse section, showing 3 locules, 6 ovules (6 other ovules beneath).

acuminate, the base rounded, the margins flat, with denticles only near apex, the veins ranked, the surfaces glabrous, polished. Inflorescence a dense complex raceme with 60 to 120 flowers, columnar; main axis arched upward, straight, stiff, of uniform width, 10–20 cm by 2–4 mm, green, smooth, polished; internodes 25 to 50, 5–10 mm long; lateral fascicles arranged in helix on main axis, each with 2 to 4 flowers and with bract subtending. Flowers trimerous; pedicel reflexed, (2–)4–6(–9) by 0.5–1 mm, smooth, glabrous, with bract subtending;

perianth cupuliform, the tepals uniform, 4.5–5.5 by 2–3 mm, yellow-green to green-white, stamens inserted at tepal base, 2–3 mm long, the filament 1.5–2.5 mm long, thin, the anther 1–1.5 mm long; ovary 2–3 by 1.5–2.5 mm, the style 1–1.5 mm long, the stigma 3-lobed, narrow. Fruits spherical, 8–9 mm in diameter, green when young, maturing to red; seeds 6 to 12, cuneate, 2.5 mm broad. Chromosome number not known.

Ecology and distribution. Rare; usually on canopy branches of oaks or *Liquidambar,* in primary cloud forests; 1350–2000 m alt. Flowering April–June, with flowers opening acropetally over 3–4 weeks; fruiting through October.

Endemic to Veracruz, Mexico.

Specimens examined. **Mexico.** Veracruz: Coacoatzintla, *Castillo 117* (F, XAL); Jico, *Chazaro 1055* (MEXU, XAL); Huitamalco, *Liebman 14635* (F, MICH); Río Jamapa, *Lot 1181* (GH); Acultzingo, *Matuda 1151* (MICH, US); Santa Rita, *Ortega 2034* (XAL); Teocelo, near Jalapa, *Pringle 7854* (GH, US); Orizaba, *Reko 72* (GH); vic. Orizaba, *Weaver 1760* (DUKE, F, MICH); vic. Atzapan, Cerro Hucapan, *Rosas 352* (GH, K, MEXU); between Atzacán and Rincón Grande, *Rosas 381* (GH, MEXU); near El Puerto, *Sharp 44709* (MEXU); between Atzacán and Dos Ríos, *Sohmer 9520* (MEXU); Magdalena, *Valdivia 2175* (XAL).

Maianthemum macrophyllum is most easily distinguished by its dense columnar inflorescences and its cupuliform flowers. As an epiphyte of primary vegetation, it may be in some danger of extinction, although it is currently cultivated in the Botanical Garden of INIREB in Jalapa, Mexico. Despite the fact that most of the locations cited above have been deforested, there are still many unexplored areas along the Veracruz-Oaxaca border with forests that are the preferred habitat for this taxon.

The tepals of *Maianthemum macrophyllum* are never reflexed, nor are they fused as in *M. henryi* of China. Hara (1975) has shown the various degrees of fusion found among the Asian species, but no New World species shows any tendency toward a fused corolla.

7. **Maianthemum monteverdense** LaFrankie, sp. nov. Figure 12, Map 2.

A speciebus aliis Maianthemii in racemo complexo pendulo, 12–20 cm longo, axe principale 2–4 mm lato, pedicello 1–2.5 cm longo, 1–1.5 mm lato, fructu 1–1.5 cm lato, semine 12, differt.

Epiphytic herb, ca. 0.8 m tall. Roots uniform, 8 to 10 per rhizome unit, evenly scattered, 30–60 cm by 1–2 mm. Rhizome a dense forking sympodium, the individual units subspherical, 4–6 cm broad, the scale leaves 8 to 10, the internodes 2–3 mm long, the lateral buds ca. 8, axillary, 1 or 2 developing as leafy shoots; epidermis replaced by periderm; starch near rhizome apex only. Leafy stem arching, 60–85 cm long, 8–12 mm broad at base, surface smooth, polished; foliage leaves 12 to 16; internodes 4–8 cm long, shorter apically. Leaves clasping or with petiole 1–2 mm long; blade ovate to lanceolate, 13–15 by 9–10 cm, the apex acute to tapered-acuminate, the base rounded, the margin flat, with denticles inconspicuous and appressed, the veins ranked, the surface glabrous, polished. Inflorescence a complex raceme (lower fascicles

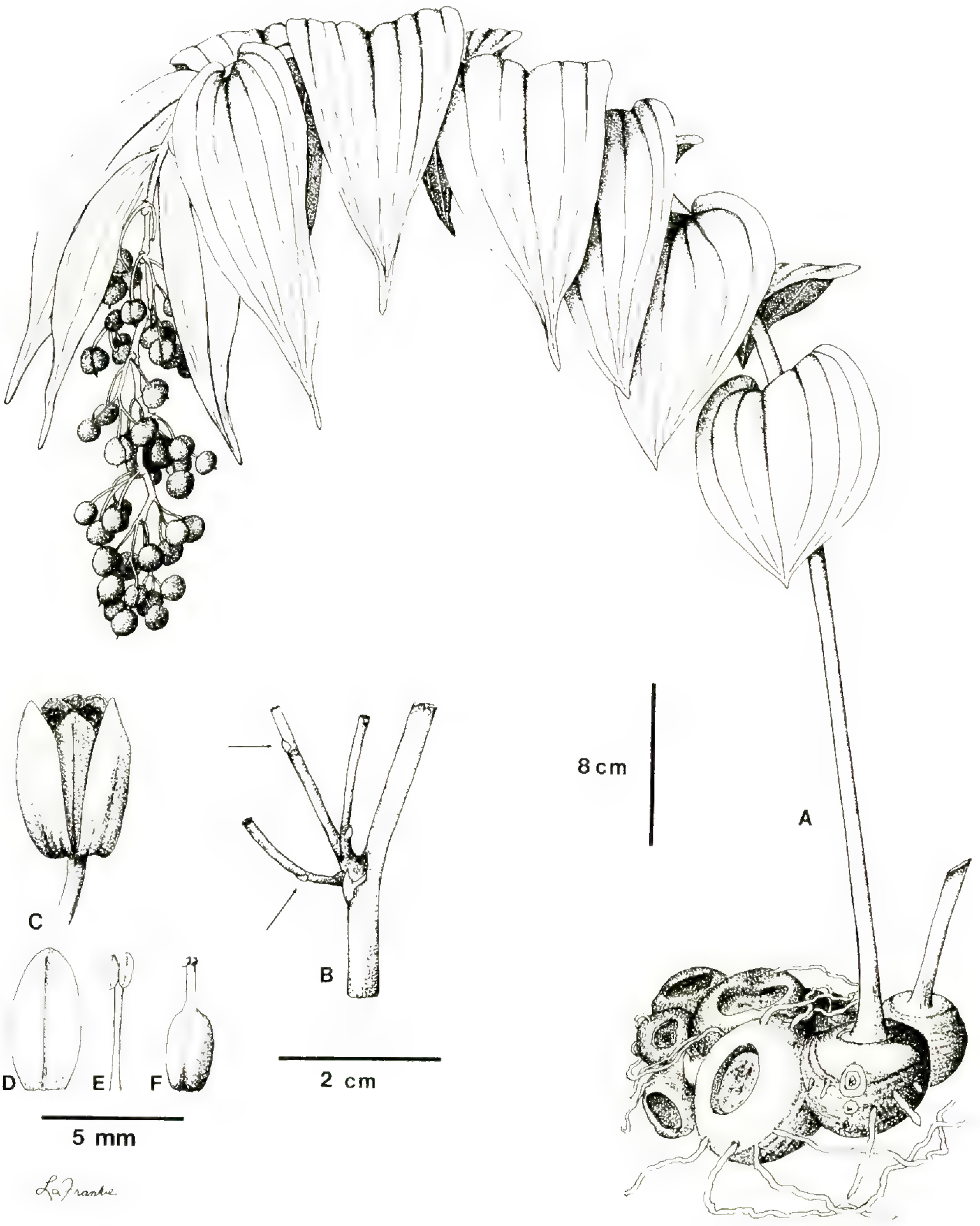


FIGURE 12. *Maianthemum monteverdense*: A, rhizome, leafy shoot, and infructescence; B, detail of lateral branch of infructescence; C, flower; D, tepal; E, stamen; F, gynoecium. (A, B based on *LaFrankie 83-IV-14B*, GH; C–F on *Luteyn 4506*, DUKE.)

sometimes congested racemes < 5 cm long) with 40 to 60 flowers; main axis pendent, slightly flexuous, 15–20 cm long, 3–5 mm broad at base, smooth, light green, polished; internodes 1–2 cm long; lateral branches in helix, spreading, with 4 to 6 flowers clustered on short axis. Flowers trimerous; pedicel 10–25 by 0.8–1.2 mm, smooth, glabrous, with bract inserted between base and midpoint; perianth cupuliform, the tepals uniform, 5–5.5 by 2 mm, yellow-green; stamens inserted at tepal base, 2–3 mm long, the filament 1.5–2 mm

long, thin, the anther oblong, ca. 1 mm long; ovary cylindrical, ca. 2 by 1 mm, the style 1.5 mm long, the stigma 3-lobed, ca. 1.5 mm broad. Fruits 3-lobed, 10–12 mm broad, green when young, maturing to red; seeds 2 to 12, slightly flattened, 1.5–2 mm wide. Chromosome number not known.

TYPE. Costa Rica, Alajuela, Monteverde Forest Preserve, Pantano Chomogo, 1600–1620 m, *Dwyer 1408* (holotype, F!).

ECOLOGY AND DISTRIBUTION. Cloud forests, persisting in blowdowns as long as canopy remains open; 1600–1700 m alt. Flowering December–February; fruits retained through August.

Relatively restricted distribution; most collections from Cordillera de Tilarán in northern Costa Rica.

SPECIMENS EXAMINED. **Nicaragua.** JINOTEGA: [northern spur of Cordillera Isabella,] Cerro San Pedro, Monte Kilambe, *P. Moreno 7516* (MO). **Costa Rica.** ALAJUELA: Reserva Forestal, San Ramón, *Carvajal 135* (MO), *346* (MO); 15 km NW of San Ramón, Cerro Azahar, *Liesner 15620* (MO); 12 km NW of San Ramón, *Judziewicz 14906* (MO); Monteverde Forest Preserve, NE section, 1600–1700 m, *LaFrankie 83-IV-14B* (GH), *Utley 2379* (F); road out of Sucre toward Pozo Verde, toward Cerro Porvenir, *Luteyn 4506* (DUKE). HEREDIA: S slope of Volcán Barba, *Hatheway 1372* (US).

The form of the lateral racemes (each consisting of a few flowers borne on long pedicels that are drawn together, with the subtending bract usually adnate and repositioned at the midpoint of the pedicel) associates this species with the more northern *Maianthemum amoenum*. Also, both species are epiphytes. However, *M. monteverdense* differs from *M. amoenum* in having a long, pendent inflorescence rather than a short, erect one and in lacking the red coloring in the central axis of the inflorescence. It is also larger in most vegetative dimensions.

8. **Maianthemum paludicolum** LaFrankie, Amer. J. Bot. **73:** 1258. 1986. TYPE: Costa Rica, Cartago, 17 km S of Empalme along Pan-American Highway, 2500 m, 22 Sept. 1985, *LaFrankie & Beach 85-23* (holotype, GH!). FIGURE 13, MAP 4.

Terrestrial herb, 1 m or more tall. Roots uniform, 2 to 4 per rhizome unit, aggregated at branch junctions, up to 60 cm by 1–2 mm. Rhizome a linear or forking sympodium, mostly exposed and upright, the individual units long-cylindrical, 10–45 cm by 7–20 mm, the scale leaves 7 to 9, the first and last internodes 2–5 mm long, middle ones 3–25 cm long, the lateral buds 2, at base of leafy shoot, axillary, 1 or 2 developing as leafy shoots; epidermis replaced by periderm; distribution of starch not known. Leafy stem upright, slightly flexuous, 35–65 cm long, 3–4 mm broad at base, glabrous; foliage leaves 9 to 12 (to 14); internodes 1.5–3 cm long. Leaves with petiole 1–2 mm long; blade ovate to lanceolate, upper ones 10–15 by 2–4.5 cm, lower ones 5–9 by 3–5 cm, the apex acuminate, the base rounded, the margin flat, entire, the veins of uniform strength, the surfaces glabrous. Inflorescence a pyramidal panicle with 40 to 80 (to 120) flowers; main axis upright, stiff, straight, tapering, 6–20 cm long, 1.5–2 mm wide at base, slightly ribbed, red-violet, glabrous; internodes

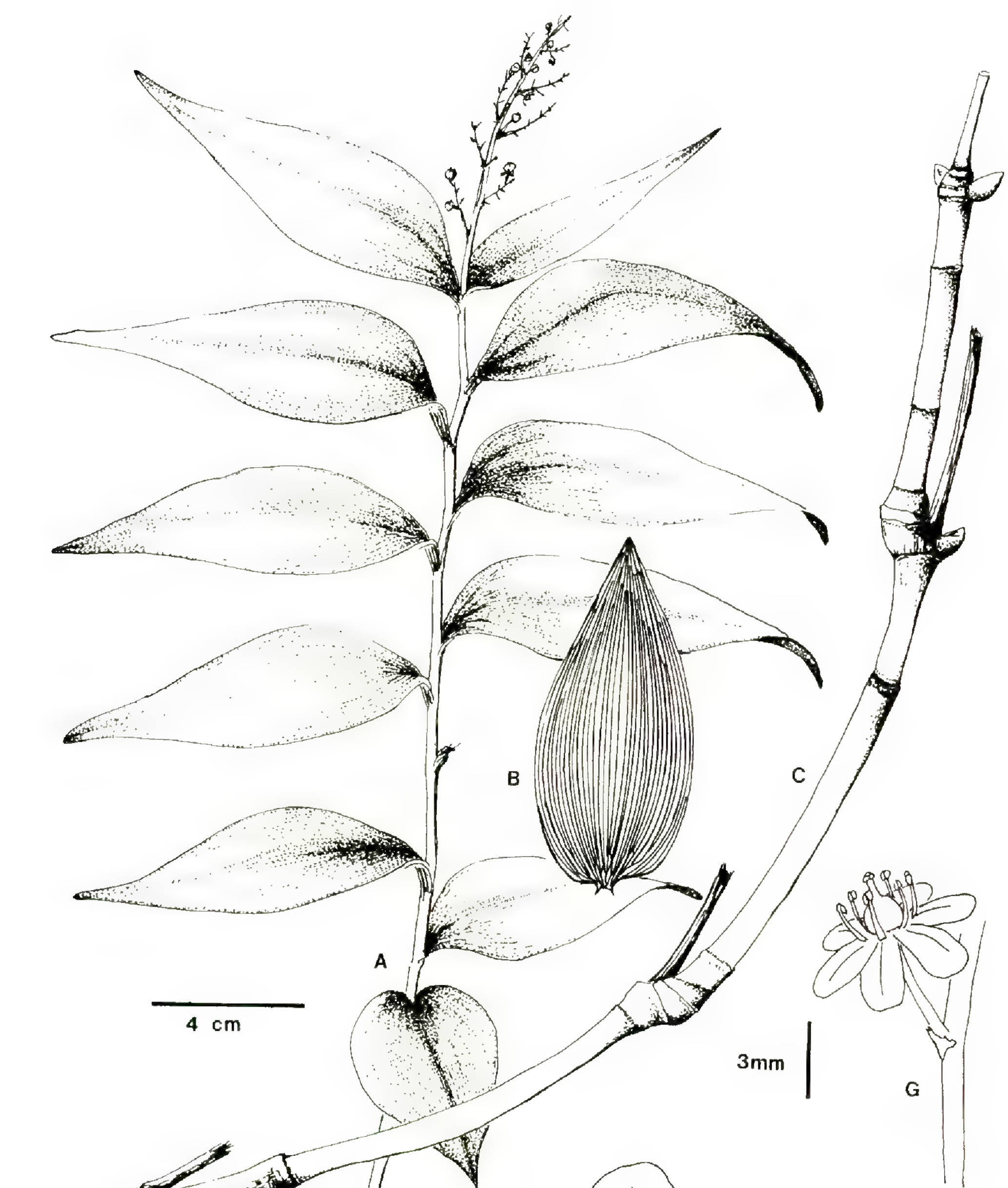


FIGURE 13. *Maianthemum paludicolum* (*Jiménez 23*, US): A, leafy shoot (note spreading leaves of uniform size); B, leaf, showing veins of uniform strength; C, sympodial rhizome, showing bases of old leafy stems, long scale-leaf internodes, renewal buds at base of leafy stem (renewal shoot and leafy shoot growing in same direction); D, tepal; E, stamen; F, gynoecium; G, flower on lateral raceme.

5 to 15, 3–10 mm long; lateral axes racemose, arranged in helix, spreading or slightly ascending, 3–8 cm long, 1 or 2 flowers at base and others at irregular intervals of 1.5–6 mm, bract subtending each lateral raceme. Flowers trimerous; pedicel 2–5 by ca. 0.5 mm, ribbed, glabrous, with bract subtending; tepals uniform, spreading, 3–4 by 1.5–2.5 mm, white; stamens inserted at tepal base, the filament 1–2 mm long, narrow, the anther 0.5–0.8 mm long; ovary spherical, 1–1.4 mm in diameter, the style ca. 1 mm long, the stigma 3-lobed, ca. 0.8 mm broad. Fruits spherical, 5–7 mm in diameter, red at maturity; seeds 1 to 3, spherical, ca. 4 mm in diameter. Chromosome number not known.

ECOLOGY AND DISTRIBUTION. Rare; alpine bogs and wet ground of central Costa Rica; 2500–2800 m alt. Flowering April–November; fruits evident throughout year.

Most frequently collected along Pan-American Highway (including powerline right of way), 10–25 km south of Empalme, but rather common throughout this open boggy site.

SPECIMENS EXAMINED. **Costa Rica.** SAN JOSÉ–CARTAGO border: 15.8 km SE of Empalme, [along Pan-Am. Highway,] *Wilbur 19907* (DUKE); 16 km SE of Empalme, *Wilbur 17546* (DUKE); 17 km SE of Empalme, *Utley 837* (F, MO); 17.6 km SE of Empalme, *Wilbur 22564* (DUKE); 18–20 km SE of Empalme, bog, *Cruz 14* (F, GH); 20 km SE of Empalme, *Burger 9553* (F), *Lellinger 1140* (F, MO, US), *Wilbur 23770* (DUKE); 9.6 mi SE of Empalme, *Wilbur 16738* (DUKE); 22 km SE of Empalme, *Burger 7985* (F, MO, NY); Ojo de Agua, *Dayton 3030* (F), *Stork 3025* (F); Río Humo, *Pochero 76* (F); Pan-Am. Highway, 8 km E of road to La Cima, *D. Stevens 13385* (F); Cerro del Muerte, sphagnum bog, *Barbour 1023* (F), *Carlson 3491* (F, GH, LL), *Carpenter 561* (US, WIS); Talamanca Range, Pacific slope, *Taylor 11807* (MO); Tres de Junio[?], Pan-Am. Highway, 2400 m, *Todzia 1323* (CR, LL).

Maianthemum paludicolum cannot be confused with the other paniculate species of Costa Rica if close attention is paid to the distinctive venation of the leaves and to their overall dimensions, as well as to the rhizome and the growth habit. The original description of this species includes an analysis of its unusual rhizome.

9. **Maianthemum paniculatum** (M. Martens & Galeotti) LaFrankie, Taxon **35:** 588. 1986. FIGURE 14, MAP 6.

Smilacina paniculata M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles **9:** 388. 1842; *Vagnera paniculata* (Martens & Galeotti) Standley, J. Wash. Acad. Sci. **15:** 457. 1925. TYPE: Mexico, Oaxaca, Chinantla, epiphytic on oaks, 2000–4000 ft, *Galeotti 5472* (holotype, BR (BR no. *3394/84-4*!)).

Tovaria thyrsoidea Baker, J. Linn. Soc., Bot. **14:** 568. 1875; *Smilacina thyrsoidea* (Baker) Hemsley, Biol. Cent.-Amer., Bot. **3:** 368. 1884. TYPE: Mexico, [Oaxaca?,] Sierra San Pedro Nolasco [Cerro de Nolasco], Talea, 1843–1844, *Jurgensen 959* (lectotype, here chosen, K!).

Tovaria nervulosa Baker, J. Linn. Soc., Bot. **14:** 569. 1875; *Smilacina nervulosa* (Baker) Hemsley, Biol. Cent.-Amer., Bot. **3:** 368. 1884. TYPE: Mexico, Veracruz, Jalapa, *Torrey 1040* (holotype, K!).

Tovaria laxiflora Baker, J. Linn. Soc., Bot. **14:** 569, 570. 1875; *Smilacina laxiflora* (Baker) Hemsley, Biol. Cent.-Amer., Bot. **3:** 368. 1884. TYPE: Guatemala, Chilascó, 1861, *Salvin & Goodman s.n.* (holotype, K!).

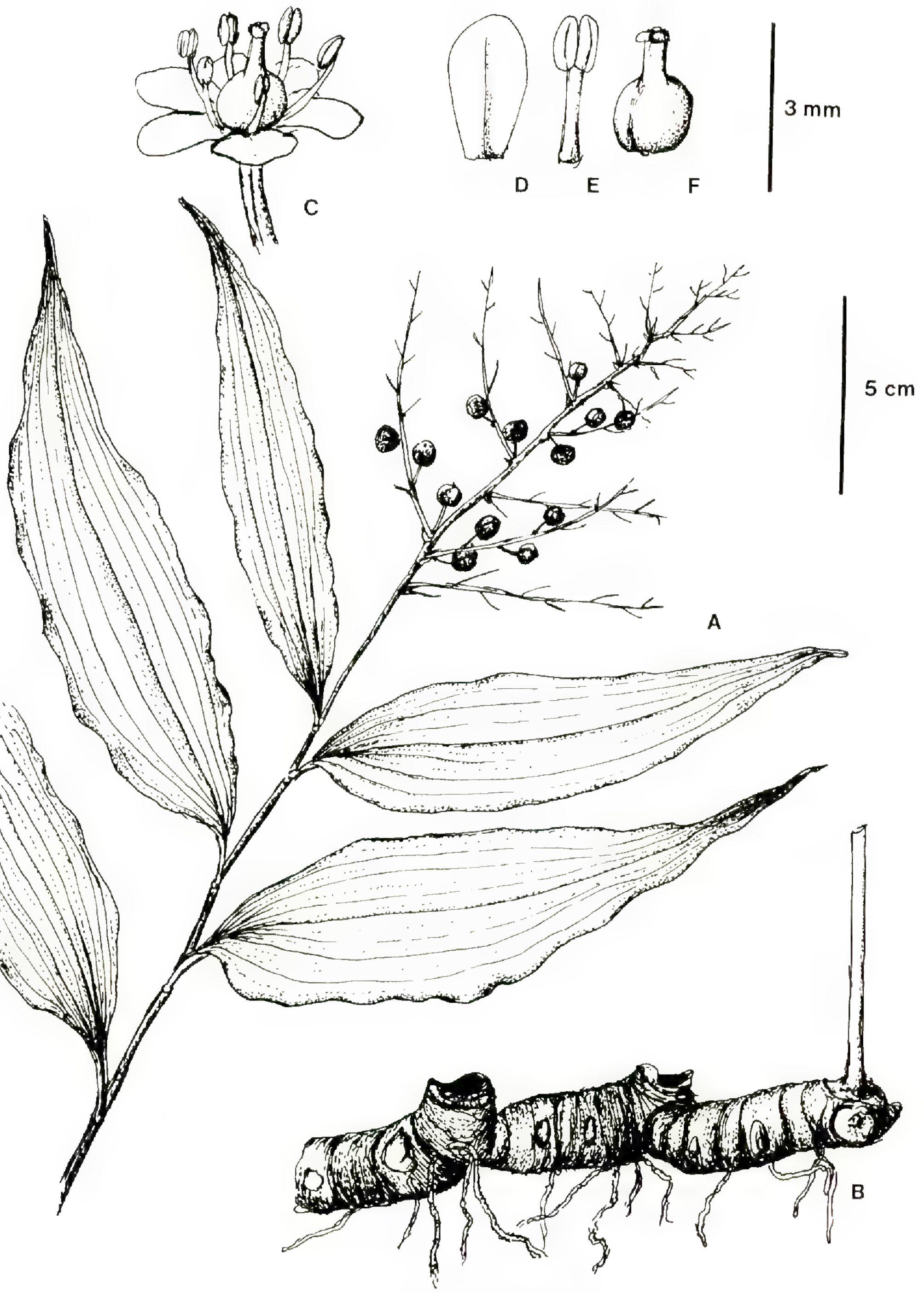
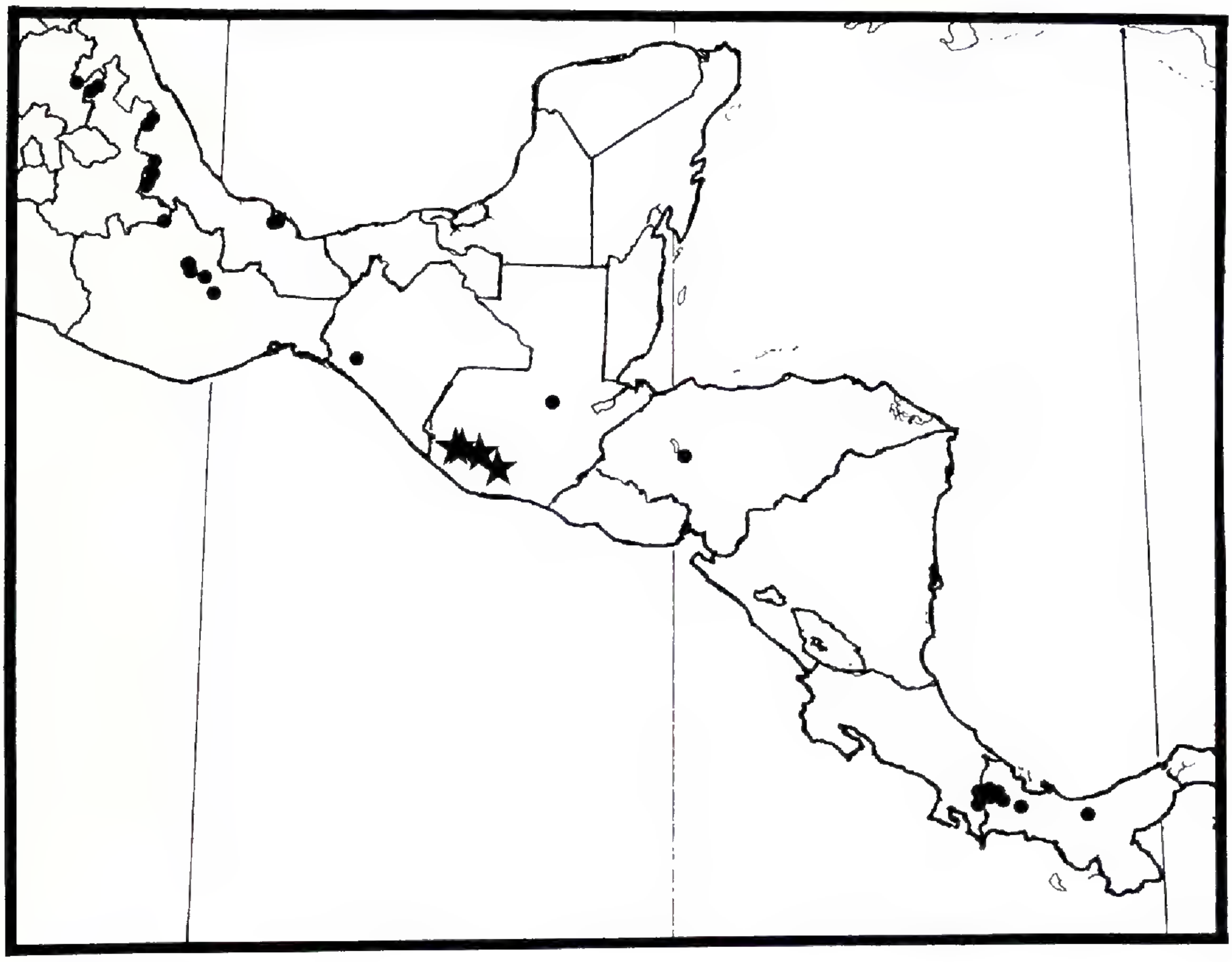


FIGURE 14. *Maianthemum paniculatum* (*LaFrankie 83-IV-20,* GH): A, upper portion of leafy shoot and infructescence (note widely spaced pedicels on lateral branch axes); B, rhizome; C, flower; D, tepal; E, stamen; F, gynoecium.



Map 6. Distribution of *Maianthemum paniculatum* (dots) and *M. salvinii* (stars).

Terrestrial forest herb, 0.7–1.5 m tall. Roots uniform, 8 to 20 per rhizome unit, evenly scattered, 30–50 cm by 1–2 mm. Rhizome a forking sympodium, the individual units short-cylindrical to narrow-claviform, 2–3.5 by 2–4 cm, the scale leaves 6 or 7, the internodes 2–12 mm long, shorter apically, the lateral buds 6, axillary, 1 or 2 developing as leafy shoots; epidermis replaced by periderm; starch deposited in distal portions but not dense. Leafy stem arching, leaning, or upright, 75–150 cm long, 6–8 mm broad at base, the surface smooth, glabrous; foliage leaves 10 to 15; internodes 4–6.5 cm long. Leaves with petiole 4–6 mm long; blade ovate-elliptic, 10–14 by 4–6 cm, the apex acuminate, the base tapered, the margin undulate, entire or denticulate, the veins ranked, the surface glabrous. Inflorescence a pyramidal panicle with 70 to 200 flowers; main axis arching upward, tapered, 15 cm long, 2–3 mm wide at base, weakly ribbed, smooth or with denticles, green or maroon; internodes 10 to 15, 8–20 cm long; lateral axes racemose, arranged in helix, spreading or ascending, 5–8 cm long, with 1 flower at base and others inserted at intervals of (7–)10–20 mm, with bract subtending each raceme. Flowers trimerous; pedicel 1–2 by ca. 0.4 mm, weakly ribbed, smooth or with denticles, with bract subtending; tepals uniform or weakly dimorphic, spreading, 2–3.2 mm long, white; stamens inserted at tepal base, the filaments thin, 1.4–2.2 mm long, the anthers 0.6–1 mm long; ovary spherical, 0.8–1.2 mm broad, style 0.6–1.4 mm long, stigma distinctly 3-lobed. Fruits spherical or weakly 3-lobed, 8–12 mm

broad, green, mottled with red when young, maturing to red; seeds 1 to 6, usually spherical, 5.5–6 mm in diameter. Chromosome number not known.

ECOLOGY AND DISTRIBUTION. Common and widespread by roadsides and in light-gaps in forest, sometimes persisting in shade. Widely distributed throughout entire range of genus in Meso-America, although absent in northern and central Costa Rica. Flowering and fruiting throughout year but less common December–March.

SPECIMENS EXAMINED. **Mexico.** HIDALGO: Tenango de Doria, 1800 m, *Gimate 966* (MEXU, MICH, MO, XAL). PUEBLA: below Honey Station, *Pringle 8836* (CAS, F, GH, LL, MICH, NY, UC, US); between Teziutlán and Tlapacoyán, *Suacedo 70* (DS, MICH, MS, WIS); N of Tlatlaqui, *Boege 1709* (MEXU). VERACRUZ: Atzalan, Tetejicapa, *Ventura 964* (DS, F, MEXU, MICH, MS); Altotonga, *Ventura 75* (DS, F, MICH, MO); Río Jamapa and road from Coscomatepec, *LaFrankie 83-20* (GH), *Lot 1170* (MEXU); 18.5 km NW of Coscomatepec, *Nee 19729* (F, XAL); 16 km NE of Huayacocotla, *Hernandez 1476* (F, MEXU), *Juarez 41* (XAL); vic. Soteapan and Volcán Santa Marta, *Beaman 5401* (MEXU, MO, XAL), *6218* (XAL), *Ortega 1056* (XAL), *1077* (XAL), *1088* (XAL), *Sousa 3609* (MEXU), *Vasquez 61* (XAL); Cerro de Villa Rica, *Castillo 1868* (XAL); Acatlán, *Ventura 9390* (MEXU). OAXACA: Rte. 175, 28 km S of Valle Nacional, 2000 m, *King 2115* (MICH), *LaFrankie 84-28* (GH); Yelagaga, Yetzuconi, *Hallberg s.n.* (MEXU). CHIAPAS: E base Cerro Tres Picos, 1500–1800 m, *Breedlove 24971* (DS, MO). **Guatemala.** BAJA VERAPAZ: on road from Cobán to Guatemala City, 3 km N of La Unión, *D. E. Stone 3523* (DUKE). **Honduras.** COMAYAGUA: near summit of El Achiote, above Siquatepeque, *Yuncker 6257* (F, GH, MICH, MO). **Costa Rica.** LIMÓN: Atlantic slope of Talamanca, near Panamanian border, *Davidse 28683* (MO); vic. Puntarenas border, Cerro Nai, *Davidse 26117* (MO); between Cerro Nai and Cerro Dudu, *Davidse 26100* (MO). PUNTARENAS: upper Río Barú, 2010 m, *L. D. Gómez 21469* (MO); headwaters of Río Bellavista, *L. D. Gómez 22641* (MO). **Panama.** BOCAS DEL TORO: headwaters of Río Culubre, border with Panama, *Davidse 25179* (MO); Valle del Silencio, *Antonio 1624* (MO). CHIRIQUÍ: vic. Volcán Chiriquí, *Davidson 990* (F, GH, MO, US), *Mori 5751* (MO, NY), *Woodson 1034* (MICH, MO, NY, US); Casita Alto, top of Cerro Copete, *Woodson 339* (CAS, GH, MO, NY, US), *341* (MO), *342* (GH, MO, NY, US); slopes of Los Cumbres near town of Cerro Punta, *Croat 13733* (MO); ridge N of Quebrada Iglesia, near town of Cerro Punta, *Croat 16071* (MO, NY); Cerro Respinga, *D'Arcy 10090* (MO), *Webster 16541* (MO); vic. New Switzerland, *Allen 1392* (GH, MO); N of San Felix, along continental divide, *Mori 5794* (MO, NY); vic. Monte Lirio, Río Chiriquí Viejo, *Seibert 184* (GH, MO, NY); 10 mi above Boquete on road to Volcán Barú, *Croat 34837* (MO); E slope Cerro Pando, *Knapp 1639* (MO); Fortuna Dam, continental divide, *D'Arcy 15950* (MO); Cerro Hornito, *Mori 7469* (MO). VERAGUAS: Cerro Tute, *Hamilton 3988* (MO), *4002* (MO).

The type of *Maianthemum paniculatum* is undoubtedly a mixed collection. There are two sheets in BR labeled *Galeotti 5472,* but since only one corresponds with the protologue and with the many other specimens annotated *Smilacina paniculata* by Martens, I have chosen this (BR no. *3394/84-4*) as the lectotype. The second sheet (BR no. *3394/84-5*) is a small plant, evidently not fully mature, with six subsessile leaves (blade oblong-ovate, apex acute). The specimen was originally annotated by Martens "*S. interius* M. Martens & Galeotti" (nomen ined.), but this name was crossed out and *S. paniculata* written below by Martens. The confusion may have occurred because the collection numbers assigned by Galeotti do not correspond to the order in which the plants were collected, but to their arrangement in the descriptive treatment; that is, all of

Galeotti's collections described under *Smilacina* have collection numbers in sequence, even though they were collected in widely separated localities.

The Mexican specimens identified by Baker as separate species are not distinct from the variable *Maianthemum paniculatum*. Two species, *Tovaria laxiflora* and *T. nervulosa,* were based on single specimens of immature plants, while the five specimens listed under *T. thyrsoidea* are easily placed in *M. paniculatum,* the type of which Baker did not see. The lectotype was chosen from the syntypes by virtue of its correspondence to the description.

The distinction between *Maianthemum paniculatum* and *M. gigas* is discussed in association with the description of the latter species, but a further note on the variation of *M. paniculatum* in Panama is warranted by the great differences in size and habit the plant exhibits there. Two forms are remarkable in their singularity yet are insufficiently known to be described at this time. The first is a very small epiphyte with a narrow, very elongate rhizome, found in the vicinity of Cerro Hornito and represented by *Folsom 7225* (MO), *Hammel 2340* (MO), and *Knapp 4215* (MO). The second is another epiphyte, this with a much-extended and sparsely flowered inflorescence bearing large cupuliform flowers and very large fruits, found in the vicinity of the Fortuna Dam site and represented by *Van der Werff 6620* (MO). This plant is also notable because it was recently collected in this area below 1000 m alt. The paniculate species of *Maianthemum* in western Panama require further study, especially with regard to fine details of the flower.

10. **Maianthemum racemosum** (L.) Link, Enum. Hort. Berol. Alt. **1**: 343. 1821.

Terrestrial forest herb, 0.75–1.25 m tall. Roots uniform, 6 to 10 (to 30) per rhizome unit, scattered but mostly near base of leafy shoot, 30–60 cm by 0.5–2 mm. Rhizome a linear, horizontal sympodium, the individual units cylindrical, 30–40 by 8–14 mm, the scale leaves 8 to 10, the internodes 5–8 mm long, shorter apically, the lateral buds 2 or 3, 2 axillary, most proximal bud displaced to lower side of rhizome, 1 (rarely 2) developing as leafy shoot; epidermis persistent; starch in immature renewal shoot only. Leafy stem simple, stiff, upright, 75–125 cm long, 7–9 mm broad at base, ribbed, pubescent or glabrous; foliage leaves 7 to 12; internodes 2.5–5 cm long, shorter apically. Leaves clasping and sessile, or with petiole 2–6 mm long; blade elliptic to ovate, 9–17 by 4.5–7.5 cm (upper ones), ovate, 9–14 by 5–8 cm (lower ones), the apex acute or caudate, the base rounded or tapered, the margin undulate, denticles distinct, the veins ranked, the surfaces pubescent or rarely glabrous. Inflorescence a pyramidal panicle with 70 to 250 flowers; main axis upright or arched upward, stiff, straight, 7–20 cm long, 2–3 mm wide at base, ribbed, green or yellow-green, pubescent or glabrous; internodes 7 to 30, 3–15 mm long; lateral axes racemose, arranged in helix, spreading or slightly ascending, 1–6 cm long, with 2 flowers at base and others at 1–4 mm intervals. Flowers trimerous; pedicel 0.5–1 mm by ca. 0.5 mm, ribbed, pubescent or glabrous, with bract subtending; perianth inconspicuous, the tepals spreading or reflexed, ca. 1 by ca. 0.5 mm, white; stamens inserted at tepal base, the filament petaloid to subpetaloid, 0.5–1 mm long, the anther 0.5–1 mm long; ovary ca. 1 by ca. 1 mm, style 0.1–0.3

mm long, stigma obscure. Fruits spherical to 3-lobed, 4–6 mm broad, green mottled with copper spots when young, maturing to translucent red; seeds up to 4, spherical, 2.5–4 mm in diameter. Chromosome number $2n = 36, 72, 144$ (Kawano & Iltis, 1966).

Key to the Subspecies of *Maianthemum racemosum*

Stem upright; leaves sessile, clasping, the base rounded, the apex of third leaf below inflorescence acute, with tip < 2 mm. ..... 10a. subsp. *amplexicaule.*
Stem arching; leaves with the petiole 2–6 mm, the base tapered, the apex of third leaf below inflorescence caudate, with tip 12–25 mm. ..... 10b. subsp. *racemosum.*

10a. **Maianthemum racemosum** subsp. **amplexicaule** (Nutt.) LaFrankie, stat. nov. FIGURE 15H, I; MAP 7.

Smilacina amplexicaulis Nutt. J. Acad. Nat. Sci. Philadelphia **7:** 58. 1834; *Smilacina racemosa* (L.) Desf. var. *amplexicaulis* (Nutt.) S. Watson, U. S. Geol. Expl. Fortieth Parallel **5:** 345. 1871; *Unifolium amplexicaule* (Nutt.) E. Greene, Bull. Torrey Bot. Club **15:** 287. 1888; *Vagnera amplexicaulis* (Nutt.) E. Greene, Man. Bot. San Francisco, 316. 1894. TYPE: United States, [Washington?,] Columbia River Woods, *Nuttall s.n.* (lectotype, here chosen, GH!).

Vagnera pallescens E. Greene, Proc. Acad. Nat. Sci. Philadelphia **1895:** 551. 1896. TYPE: no specimen cited, type not determined.

Smilacina racemosa (L.) Desf. var. *brachystyla* G. Henderson, Bull. Torrey Bot. Club **27:** 357. 1900. TYPE: United States, Washington, Yakima Co., moist banks of upper MacKenzie River, 13 June 1892, *Henderson 4843* (holotype, GH!).

Vagnera brachypetala Rydb. Bull. Torrey Bot. Club **28:** 268. 1901. TYPE: Canada, British Columbia, Glacier at the "Loup," Aug. 1897, *Van Brunt s.n.* (holotype, NY).

Smilacina amplexicaulis Nutt. var. *glabra* Macbr. Contr. Gray Herb. n.s. **56:** 18. 1918; *Smilacina racemosa* (L.) Desf. var. *glabra* (Macbr.) St. John, Contr. Bot. State Coll. Wash. **20:** 97. 1929; *Vagnera amplexicaulis* (Nutt.) E. Greene var. *glabra* (Macbr.) Abrams, Ill. Fl. Pacific States **1:** 453. 1923. TYPE: United States, California, Tulare Co., South Fork of Raweah River, 22 July 1904, *Culbertson 4252* (holotype, GH!).

Smilacina amplexicaulis Nutt. var. *jenkinsii* B. Boivin, Canad. Field-Naturalist **65:** 14. 1951; *Smilacina racemosa* (L.) Desf. var. *jenkinsii* (B. Boivin) B. Boivin, Phytologia **42:** 16. 1979 (including *S. amplexicaulis* var. *ovata*). TYPE: Canada, Alberta, Beaverlodge, Saskatoon Mtn., 26 June 1949, *Jenkins 730a* (holotype, DAO!).

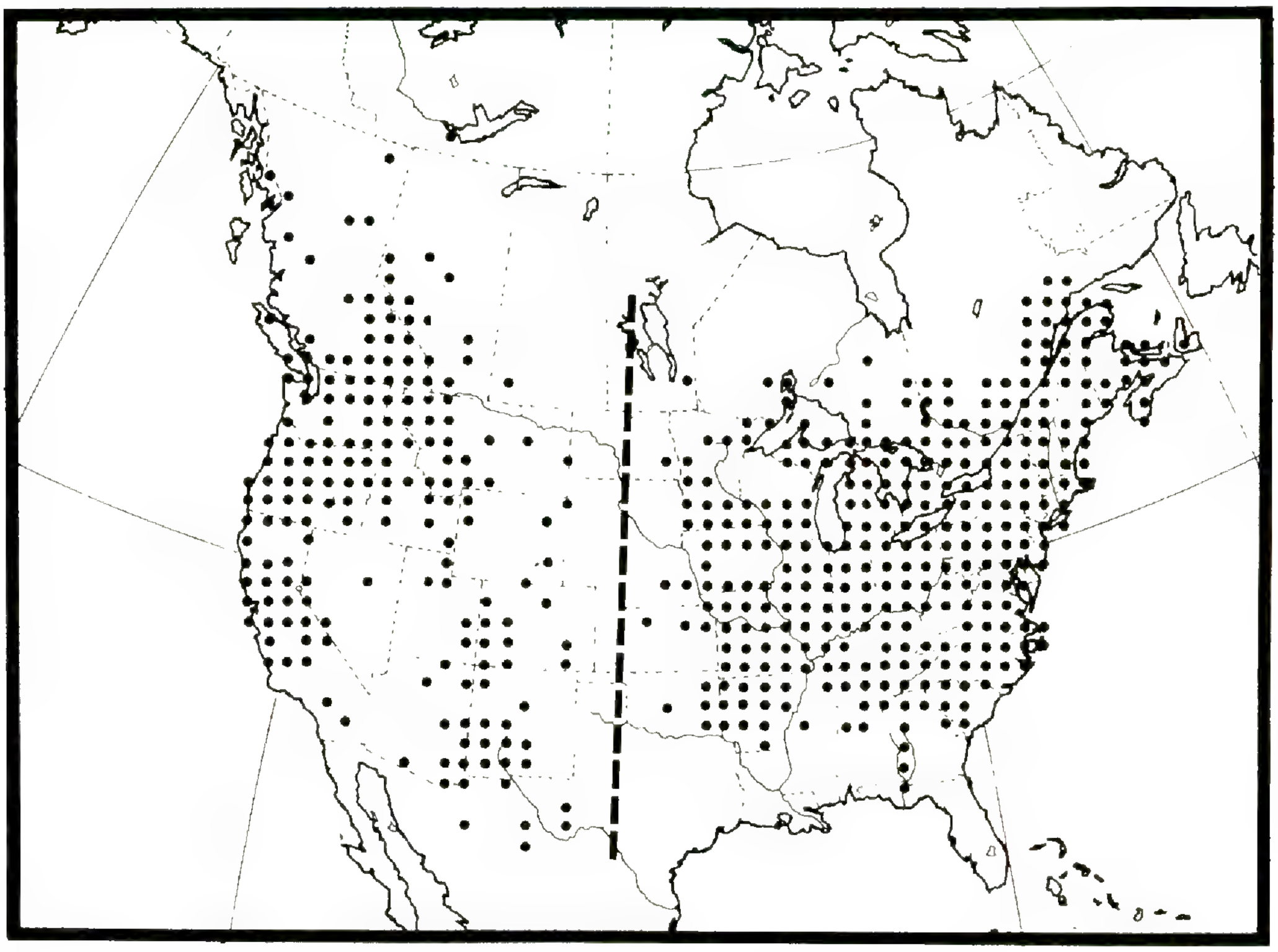
Smilacina amplexicaulis Nutt. var. *ovata* B. Boivin, Canad. Field-Naturalist **65:** 15. 1951. TYPE: Canada, Saskatchewan, Cypress Hills, aspen woods, 3700 ft, 2 Aug. 1947, *Breitung 5241* (holotype, DAO!).

Terrestrial forest herb, 0.75–1.25 m tall. Leafy stem simple, stiff, upright, 75–125 cm long. Leaves clasping, sessile; blade with the apex acute, tip extending less than 2 mm, the base rounded, the surfaces pubescent, rarely glabrous. Chromosome number $2n = 36$ (Kawano & Iltis, 1966).

ECOLOGY AND DISTRIBUTION. Common and abundant in forests and open woodlands; sea level to 700 m alt. in Northwest, over 3000 m alt. in Chihuahua Range in northern Mexico. Shoots produced annually; flowering May–June; fruits retained through September or October.

Like its eastern counterpart, *Maianthemum racemosum* subsp. *amplexicaule* has broad ecological amplitude, reflected in wide latitudinal distribution. East-

FIGURE 15. *Maianthemum racemosum*. A–G, subsp. *racemosum*: A, rhizome, renewal shoot right, abscission scars of old shoots left; B, upper portion of leafy shoot and infructescence; C, third leaf below inflorescence, showing attenuate-acuminate apex and tapered base; D, flower; E, tepal; F, stamen; G, gynoecium. H, I, subsp. *amplexicaule*: H, third leaf below inflorescence, showing acute apex and rounded base; I, leafy shoot, showing clasping leaves. (A, B, D–G based on *LaFrankie 82-VII-24A* (GH); C on TRT no. *133604*, TRT; H on *Smith & Wang 48*, GH.)



MAP 7. Distribution of *Maianthemum racemosum*. Dashed line divides eastern subspecies (subsp. *racemosum*) from western (subsp. *amplexicaule*).

ern limit in foothills of Rockies, from Saskatchewan (Cypress Hills Park, *MacLean s.n.* (GH, PH)) south through Colorado (Mesa Co., 10–12 mi SW of Glade Park, *Pennell 22104* (GH)) and New Mexico (Otero Co., Sacramento Mtns., *Worthington 6215* (LL)) to Texas (Jeff Davis Co., Mt. Livermore, *Hinckley s.n.* (GH, LL)). Southern limit includes some outlying locations in Mexico (Chihuahua, Río de Bavispe, *S. White 3283* (US); Sierra Madre, *Pringle 8036* (GH, MEXU, US)) and extends to southern California (San Bernardino Co., San Bernardino Mtns., below Bear Valley Dam, *Ewan 2756* (CAS)), but species differs from *M. stellatum* in being largely absent from Great Basin. Northern limit from central Alberta (Jasper Park, *Moss 4650* (GH, WS)) to lower coast of Alaska, with few outlying locations in northern British Columbia (Wicked R., near Peace R., *Raup 4235* (CAN, GH)). Western limit in Coast Ranges of Pacific shore.

The western subspecies of *Maianthemum racemosum* is distinguishable from the eastern subspecies by its upright habit, clasping leaves, and short-acute leaf apex; these differences can be seen in the color photographs in Rickett (1966, *pl. 6*; 1972, *pl. 8*). Some plants intermediate between the two subspecies are found in the region between southeastern British Columbia and northern Idaho. There are only a few chromosome counts available for subsp. *amplexicaule,* but all report a diploid number of 36, indicating that this subspecies may have a more stable karyotype than does the eastern subspecies.

10b. **Maianthemum racemosum** subsp. **racemosum** FIGURE 15A–G, MAP 7.

Convallaria racemosa L. Sp. Pl. 315. 1753; *Tovaria racemosa* (L.) Necker ex Baker, J. Linn. Soc., Bot. **14:** 565. 1875; *Polygonastrum racemosum* (L.) Moench, Methodus, 637. 1794; *Unifolium racemosum* (L.) Britton, Trans. New York Acad. Sci. **8:** 74. 1889; *Vagnera racemosa* (L.) Morong, Mem. Torrey Bot. Club **5:** 114. 1894; *Smilacina racemosa* (L.) Desf. var. *typica* Fern. Rhodora **40:** 406. 1938. TYPE: [United States, Virginia?,] collector and number not known (lectotype, BM; photograph in Rhodora **40:** *pl. 512.* 1938).

Smilacina ciliata Desf. Ann. Mus. Natl. Hist. Nat. **9:** 53. *t. 9.* 1807; *Convallaria ciliata* (Desf.) Poiret, Encycl., Suppl. **4:** 30. 1816. TYPE: not determined.

Smilacina flexicaulis Wender. Schriften Ges. Beförd. Gesammten Naturwiss. Marburg **2:** 249. 1839. TYPE: [origin not known; cultivated in the Botanical Garden, Marburg] (lectotype, here chosen, protologue).

Vagnera retusa Raf. Autik. Bot. 68. 1840. TYPE: Allegheny Mtns., *Rafinesque s.n.* (holotype, PH?, probably destroyed; lectotype, here chosen, protologue).

Vagnera australis Rydb. *in* Small, Fl. S. E. United States, 270. 1903. TYPE: United States, Alabama, Auburn, 22 April 1896, *Earle & Underwood s.n.* (holotype, NY!).

Smilacina racemosa (L.) Desf. f. *foliosa* Marie-Vict. Contr. Lab. Bot. Univ. Montréal **14:** 15. 1929. TYPE: Canada, Québec, environs de Québec, Aug. 1922, *Victorin 16009* (holotype, MT!).

Smilacina racemosa (L.) Desf. var. *cylindrata* Fern. Rhodora **40:** 406. 1938. TYPE: United States, Virginia, Princess Anne Co., Little Neck, dry mixed woods, 8, 9 Aug. 1934, *Fernald & Long 3859* (holotype, GH!; isotype, PH!).

Smilacina racemosa (L.) Desf. var. *lanceolata* B. Boivin, Canad. Field-Naturalist **65:** 15. 1961. TYPE: Canada, Ontario, Carleton, Junction Gore, railroad embankment, 30 May 1939, *Minshall 74* (holotype, DAO).

Terrestrial forest herb, 0.75–1.25 m tall. Leafy stem arching, thus presenting foliage leaves in horizontal plane, 75–100 cm long. Leaves with petiole 2–6 mm long; blade with the apex long-caudate, 12–28 mm long, the base rounded or tapered, the surfaces pubescent, more densely so abaxially. Chromosome number $2n = 36, 72, 144$ (Kawano & Iltis, 1966).

ECOLOGY AND DISTRIBUTION. Common and abundant throughout deciduous forests of eastern United States; broad tolerance with regard to water, temperature, and light (Curtis, 1959); in wet, mucky, seasonally inundated forests and river bottoms, and in dry oak-pine forests; generally restricted to deciduous or semideciduous woods, becoming most abundant along borders and light-gaps.

Eastern limit from New Brunswick (York Co., Douglas, *Roberts 59-455* (CAN)) and Nova Scotia (Lunenburg Co., Bridgewater, *Fernald & Long 23650* (GH)) south through South Carolina (Charleston Co., *Moldenke 1195a* (PH)) to mountains of Georgia (Clark Co., Ocone Heights, *Miller 2329* (PH); Bartow Co., Boston Creek, *Forman G31* (PH); Early Co., above Chattahouchee R. near Hilton, *Thorne & Muenscher 2929* (GH)) and site in Florida (Gadsden Co., below River Junction, W side St. Road 269, S of Flat Creek, *Gholson & Baker s.n.* (voucher 10855, "Flora of Florida," FTG)). Southern limit extending west through north-central Alabama (Winston Co., near Franklin Co. line, 14 mi ENE of Haleyville, *Iltis 20190* (WIS); Clay Co., Talladega Natl. Forest, *Whetstone 9930* (GH)), to northern Mississippi (Monroe Co., 6 mi NW of Amory,

Schuster 38246 (DUKE)), with single site in northern Louisiana (Claiborne Parish, ca. 3 mi E of Summerfield, *Thieret 24686* (USL)). Northern range limited by boreal spruce-fir forest; growing along rivers in deciduous coves and alder thickets, yielding oddly scattered distribution from Québec (Timiskaming Co., Ville Marie, lakeshore, *Baldwin & Breitung 4420* (CAN)) west through Ontario (Mt. Chemines, *Tynell 4907* (WAT)) to southern Manitoba. Western range extending into prairies wherever river-bottoms forested and as far south as Oklahoma (Adair Co., 1 mi W of St. Road 51 and U. S. Highway 59, *Perino & Pierson 180* (LL); Delaware Co., Dripping Springs, *Wallis 5586* (LL); Leflore Co., S of Big Cedar, *Correll 34361* (LL)).

Fernald (1938) satisfactorily lectotypified *Maianthemum racemosum* on one of two specimens in the Clifford Herbarium at the British Museum (Natural History) and published a photograph of the lectotype. Fernald did not see the specimen of *M. racemosum* at LINN, which is annotated by Linnaeus (the specimens at BM are not), but it is very much like the specimen at BM. Linnaeus had no doubt been familiar with the species for some time; it had been cultivated in Europe since the seventeenth century (Aiton, 1814), and in 1737 he had described it in his *Hortus Cliffortianus.* The material on which Desfontaines based the name *Smilacina ciliata* was cultivated in Paris, and a specimen may still be in Desfontaines's herbarium, which was transferred to FI. The illustration and description do not indicate any significant difference from *M. racemosum.*

Despite the many specific, varietal, and form names provided for the subspecies, it is quite uniform in significant characters, and I have followed Galway (1945) in reducing all the varietal names to synonymy. This morphological constancy is more remarkable in light of the wide geographic range of *Maianthemum racemosum* and the relatively greater morphological variation exhibited by other species of *Maianthemum,* especially those of the tropical mountains.

The eastern subspecies is obligately apomictic (Gorham, 1953) and cytologically diverse (Kawano & Iltis, 1966). In all of the populations of the eastern United States that I have examined, the seeds are polyembryonic, which further indicates widespread apomixis.

11. **Maianthemum salvinii** (Baker) LaFrankie, Taxon **35:** 588. 1986.

FIGURE 16, MAP 6.

Tovaria salvinii Baker, J. Linn. Soc., Bot. **14:** 568. 1875; *Smilacina salvinii* (Baker) Hemsley, Biol. Cent.-Amer., Bot. **3:** 368. 1884; *Vagnera salvinii* (Baker) Standley, J. Wash. Acad. Sci. **15:** 457. 1925; *Smilacina amoena* H. L. Wendl. var. *salvinii* (Baker) Emons, Ann. Missouri Bot. Gard. **32:** 404. 1945. TYPE: Guatemala, Volcán de Atitlán, 9000 ft, *Salvin s.n.* (holotype, K!).

Epiphytic herb, 0.75–1 m tall. Roots uniform, length not known, ca. 2 mm broad, distribution not known. Rhizome not seen. Leafy stem straight or arching, ca. 1 m long, ca. 5 mm broad at midlength, ribbed, glabrous; foliage leaves more than 7; internodes 2–4 cm long, shorter apically. Leaves with petiole 2–5 mm long; blade elliptic to lanceolate, 15–23 by 5–7.5 cm, the apex acuminate, the base rounded or long-tapered, the margin flat, entire, the veins ranked, the

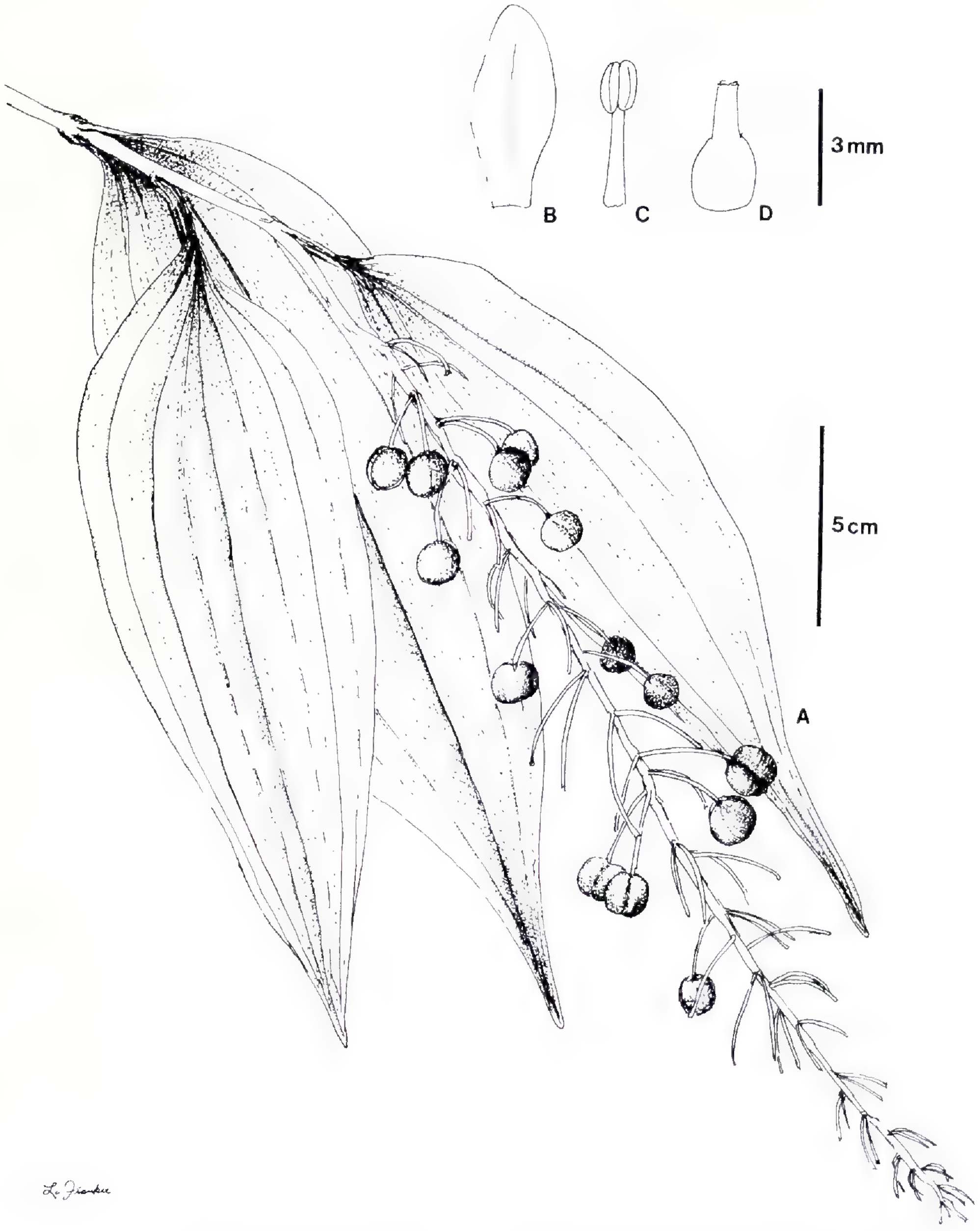


FIGURE 16. *Maianthemum salvinii*: A, upper portion of leafy shoot and infructescence; B, tepal; C, stamen; D, gynoecium. (A based on *Standley 85045*, F; B–D on *Standley 68691*, F.)

surfaces glabrous. Inflorescence a complex raceme with 120 to 150 flowers; main axis pendent, straight, 14–35 cm long, 1.3–2 mm broad at base, ribbed, color not known, glabrous; internodes 25 to 40, most ca. 5 cm long; fascicles arranged in helix, with 3 or 4 flowers, slightly reflexed and drooping, bract subtending each fascicle. Flowers trimerous; pedicel 15–25(–30) by 0.5–0.8 mm, ribbed, glabrous, with bract subtending; perianth cupuliform, the tepals uniform, spreading, 4–4.5 by 2–2.5 mm, pale pink to lavender; stamens inserted

at tepal base, the filament ca. 2 mm long, thin, the anther 0.5–1.1 mm long; ovary spherical, ca. 1 mm in diameter, style 1.5–2 mm long, stigma obscure. Fruits spherical, 8–10 mm in diameter, red at maturity; seeds 3 to 12, oblong, ca. 3 by 2 mm. Chromosome number not known.

ECOLOGY AND DISTRIBUTION. Very rare, possibly extinct; primary forests on white sand slopes; 1800–2200 m alt. Flowering in March; fruits retained through January or February.

Endemic to Guatemala.

SPECIMENS EXAMINED. **Guatemala.** SAN MARCOS: Barranca Eminencia, above San Rafael Pie de la Cuesta, 2100–2400 m, *Standley 68691* (F); near Aldea Fraternidad, between San Rafael Pie de la Cuesta and Palo Gordo, 1800–2400 m, *L. O. Williams 25685* (F). QUEZALTENANGO: El Pocito, S of San Martín, Chile Verde, 2200 m, *Standley 85045* (F); above Mujulia, S of San Martín, Chile Verde, 1800 m, *Standley 85497* (F).

Maianthemum salvinii was not recognized as a distinct species by Emons (1945). Standley annotated two of the specimens listed above as *Smilacina flexuosa* and one as *S. paniculata*. Emons annotated only one of the specimens, listing it as the hybrid *S. flexuousa* × *amoena*. The four specimens are distinguished from all other species in Central America in having long, strictly racemose inflorescences, long pedicels, and large, cupuliform, rose-colored flowers. With these flowers and the large, pendent inflorescence, *Maianthemum salvinii* is possibly the most spectacular of the Central American species of *Maianthemum*.

12. **Maianthemum scilloideum** (M. Martens & Galeotti) LaFrankie, Taxon **35:** 588. 1986. FIGURE 17, MAP 8.

Smilacina scilloidea M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles **9:** 388. 1842; *Tovaria scilloides* (M. Martens & Galeotti) Baker, J. Linn. Soc., Bot. **14:** 567. 1875. TYPE: Mexico, Oaxaca, Cerro San Felipe, *Galeotti 5471* (lectotype, here chosen, BR (BR no. *3394-84-9*!); isolectotypes, BR (BR nos. *3394/84-8*! and *3394/84-10*!), K!).

Smilacina scilloidea M. Martens & Galeotti var. *acutifolia* M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles **9:** 388. 1842. TYPE: Mexico, Oaxaca, [Sierra Madre Oriental,] Cordillera Orientale, *Galeotti 5483* (not *Galeotti 5471* as in protologue) (lectotype, here chosen, BR (BR no. *3394/84-12*!); isolectotypes, BR (BR no. *3394/84-11*!), K!, NY!, US!).

Smilacina scilloidea M. Martens & Galeotti var. *rosea* Emons, Ann. Missouri Bot. Gard. **32:** 406. 1945. TYPE: Guatemala, Volcán Santa María, *Skutch 869* (holotype, F!; isotype, US!).

Terrestrial forest herb, 15–35 cm tall. Roots uniform, 15 to 35 per rhizome unit, at nodes and internodes, mostly clumped near base of leafy shoot, 10–15 cm by 0.5–1 mm. Rhizome a long sympodium, forking, spreading widely, the individual units narrow-cylindrical, 5–10 cm by 4–8 mm, slightly flattened, the scale leaves 8 or 9, the internodes 6–14 mm long, shorter distally and apically, the lateral buds 5 or 6, axillary, 1 or 2 (rarely 3) developing as leafy shoots; epidermis replaced by periderm; starch only near rhizome apex. Leafy stem upright, 15–30 cm long, 3–4 mm broad at base, surface smooth or ribbed,

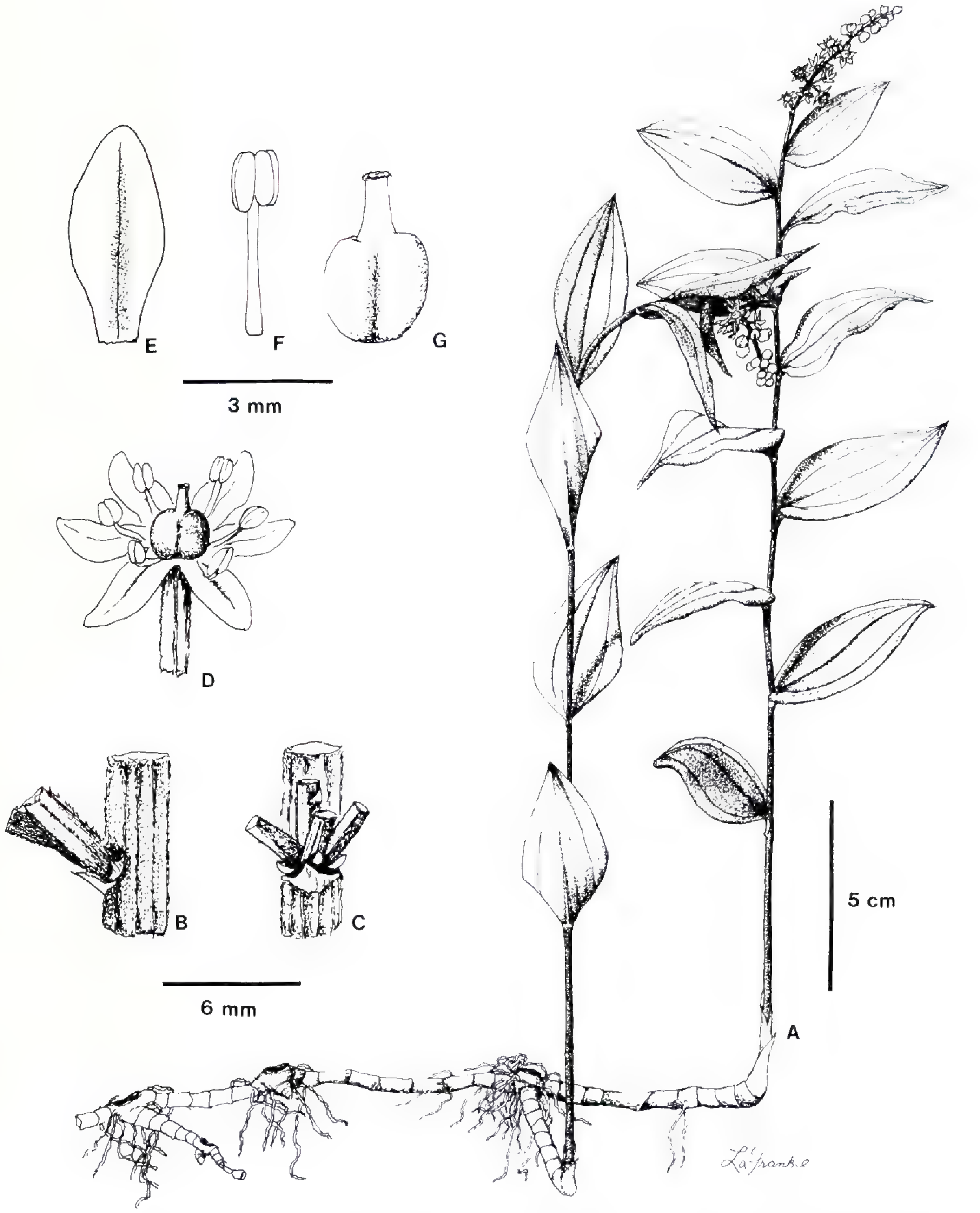
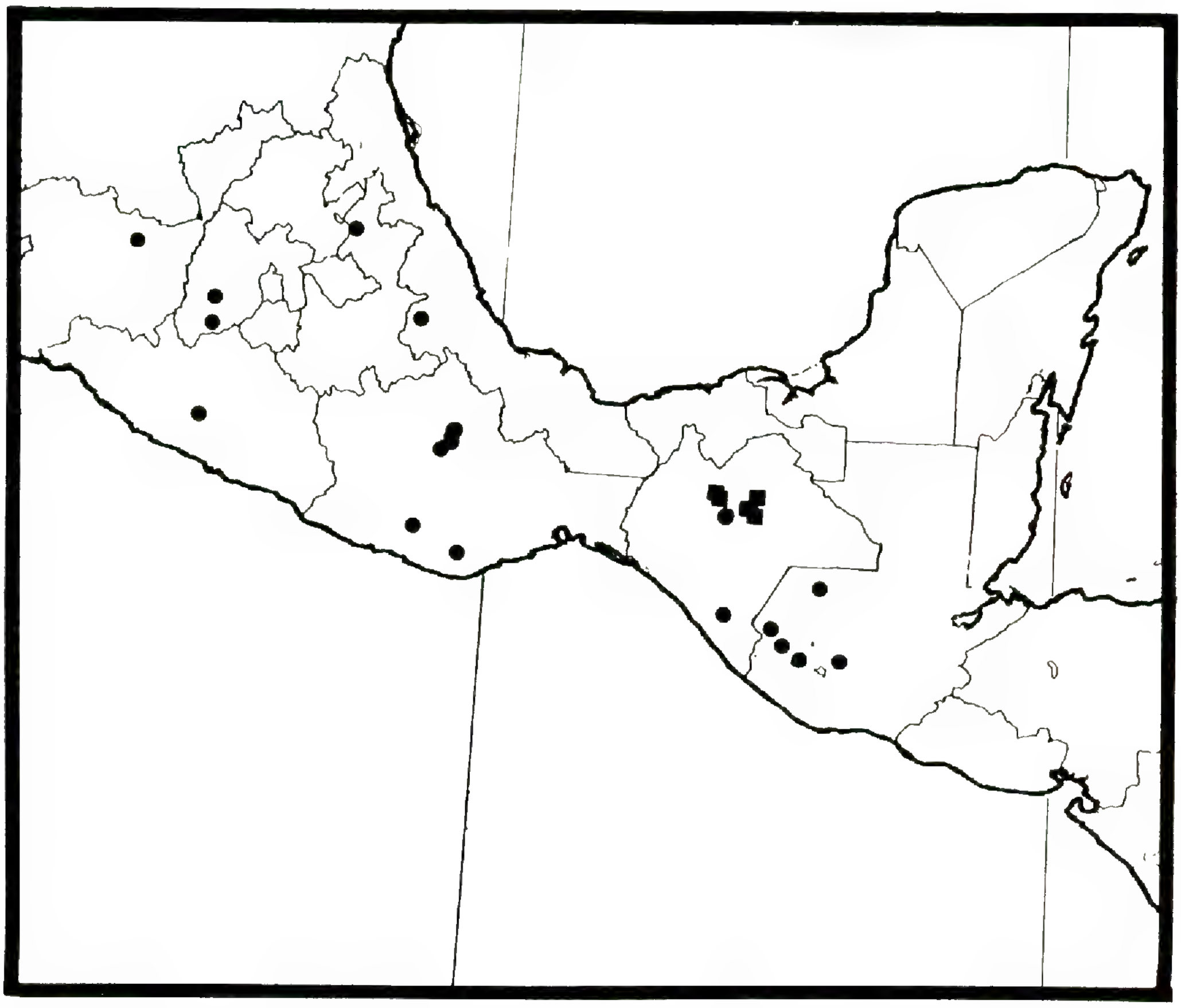


FIGURE 17. *Maianthemum scilloideum* (*LaFrankie 83-IV-24A*, GH): A, rhizome, leafy shoot, and inflorescence; B, C, lateral fascicles of inflorescence, showing 2 and 4 pedicels; D, flower; E, tepal; F, stamen; G, gynoecium.

glabrous; foliage leaves 6 to 9; internodes 2.5–5 cm long, shorter apically. Leaves sessile and clasping, or with petiole 2–3 mm long; blade elliptic to ovate, 5–8 by 2–3.5 cm, the apex short-acuminate, the base rounded, the margin flat, with denticles distinct, the veins ranked, the surfaces glabrous. Inflorescence a complex raceme with 8 to 27 flowers; main axis drooping at first, upright when



MAP 8. Distribution of *Maianthemum scilloideum* (dots) and *M. septifolium* (squares).

mature, straight, 1.5–4 cm long, 1–1.5 mm broad at base, ribbed, green or maroon, glabrous or sometimes with denticles; internodes 4 to 8, 2–7 mm long; fascicles arranged in helix, with 2 or 3 (or 4) flowers, spreading, with bract subtending each fascicle. Flowers trimerous; pedicel 3.5–8 by 0.4–0.6 mm, ribbed, glabrous or rarely with denticles, with bract subtending; tepals uniform, spreading, 3–6 by 1–1.5 mm, white; stamens inserted at tepal base, the filament 1–1.5 mm long, thin, the anther 0.5–1 mm long; ovary cylindrical, 1–1.8 by 1 mm, the style ca. 1 mm long, the stigma 3-lobed, 0.3–0.4 mm broad. Fruits spherical, 6–8 mm in diameter, green when young, maturing to red; seeds 1 to 3, spherical, 4–5 mm in diameter. Chromosome number not known.

ECOLOGY AND DISTRIBUTION. Clonal, forming loose, spreading patches in understory of conifer-oak forests; 1700–3500 m alt. Shoots usually developing on annual cycle; flowering April–August; fruits retained June–December.

Historically, as far to northwest as Michoacán; presently, scattered occurrences in Guerrero and along Pacific coastal ranges, but most common from Sierra de Ixtlán of Oaxaca to the northern highlands of Chiapas, and in scattered alpine sites in Guatemala.

SPECIMENS EXAMINED. **Mexico.** MICHOACÁN: Cerro Azul, *Arsène 5766* (GH, MO, NY, US); vic. Morelia, *Arsène 5803* (US). MÉXICO: Temascaltepec, *Hinton 886* (MICH, NY, UC, US), *4520* (F, GH, NY, US), *5079* (F, NY), *7953* (F, LL, MO, NY, TEX, US), *Matuda 31991* (MEXU); Galeana, *Hinton 14227* (GH, MICH, NY, US), *14290* (GH, LL, MO, NY, TEX, US); Yesceros, *Hinton 14407* (F, GH, LL, NY, TEX, US); 5 km S of Sultepec, *Rzedowski 30796* (MEXU); Cerro de Pinal, *Matuda 31888* (MEXU). PUEBLA: W slopes below Puerto-del-Aire, *C. Smith 3928* (F, MEXU, US); vic. Huauchinango, *Sharp 45394* (TENN). VERACRUZ: Lomagrande, vic. Orizaba, *Balls B4350* (GH, MS, NY, UC, US); Planta el Pie, Chiconquiaco, *Ventura 7018* (CAS); El Puerto, *Sharp 44709* (NY, TENN); 3 km NE of Nueva Vaquera, *Calzada 5917* (XAL); intersection of Rte. 175 and road to Puerto-del-Aire, *Horvitz 39841* (XAL). OAXACA: Cerro San Felipe, *Galeotti 5471* (BR), *5483* (BR, NY, US), *Gonzales 704* (GH, US), *Pringle 4647* (GH, MEXU, MICH, NY, UC, US); 27 km N of Ixtlán [on Rte. 175], *LaFrankie 83-30* (GH), *Roe 1964* (DS, F, MICH, WIS); 25 km N of Ixtlán, *Rzedowski 30653* (LL, MICH), *Taylor 2415* (DUKE); 12 km N of Ixtlán, *McPherson 826* (CAS, MICH); 30 km NE of Oaxaca, *Conrad 3118* (GH, MO); 7 mi NE of Oaxaca, *Webster 11508* (GH, MS); vic. Zempoaltepec, *Hallberg 820* (MEXU, MICH), *E. Nelson 667* (US); San Miguel, *Reko 3840* (US); 35 km S of Juchatengo, *Roe 580* (F, WIS); 21.9 mi S of Suchixtepec, *Croat 46100* (MEXU); 3 km S of San José del Pacífico, *Ortega 1767* (XAL). GUERRERO: 4 mi W of Omiltemi, *Wilkinson 3371* (MEXU, MICH); 3 mi W of Omiltemi, *Hamilton 3262* (MEXU, MICH); N slope of Cerro Alquitrán, *Anderson 4446* (MICH); 5 km W of Camotlá, *Sanchez s.n.* (MEXU); 18 km S of Filo de Caballo, *Rodriguez 85* (MEXU). CHIAPAS: Cerro Huitepec, *Alexander 1135* (MEXU, MICH, US), *Breedlove 23023* (DS, MICH, MO, NY), *Laughlin 1027* (CAS, MEXU, UC, WIS), *1853* (DS); Cerro Zontehuitz, *Breedlove 6662* (DS, US); Santa Rosa, near Escuintla, *Matuda 4256* (GH, LL, MEXU, NY); Volcán Tacaná, *Matuda 2365* (GH, MEXU, MICH). **Guatemala.** HUEHUETENANGO: between San Mateo Ixtatán and Nucá, *Steyermark 49842* (F, US); vic. Tunima, *Steyermark 48412* (F, NY, US); Cerro Pixpix, *Steyermark 50561* (US). QUEZALTENANGO: Volcán Zunil, *Steyermark 34720* (F, MO); Volcán Santa María, *Skutch 869* (F, GH, US). SAN MARCOS: 4.4 mi W of Ixchiguan, *Beaman 3244* (GH, LL, MS, UC, US); between San Marcos and Serchill, *Standley 85391* (F, US), *85418* (F). CHIMALTENANGO: Volcán Acatenango, *Standley 61890* (F).

Among the duplicates at BR, one set of specimens evidently received full printed labels and contains handwritten notes by Martens concerning location and floral morphology; I have chosen these as the lectotypes. The duplicates have different labels or none at all, and usually have much-abbreviated label annotations. The type material under this species is all very uniform, unlike the situation with *Maianthemum paniculatum*.

The distinction between *Maianthemum scilloideum* and *M. flexuosum* is presented under the discussion of the latter species. In general, *M. scilloideum* is a diminutive plant of higher mountains, and it is not easily confused with any other species.

13. **Maianthemum septifolium** LaFrankie, sp. nov. FIGURE 18, MAP 8.

A speciebus aliis Maianthemii in foliis 6 ad 8 (ad 10), rhizomate angusto, elongato, cylindrico vel leviter complanato, 2–5.5 cm longo, 0.8–1.4 cm lato, inflorescentia plerumque paniculata, petalis 2–4 mm longis, 1.2–2 mm latis, differt.

Terrestrial forest herb, 45–75 cm tall. Roots uniform, 10 to 20 per rhizome unit, scattered at nodes and internodes, 15–35 cm by 1.5–2 mm. Rhizome a dense or spreading, forking sympodium, the individual units narrow-cylindri-

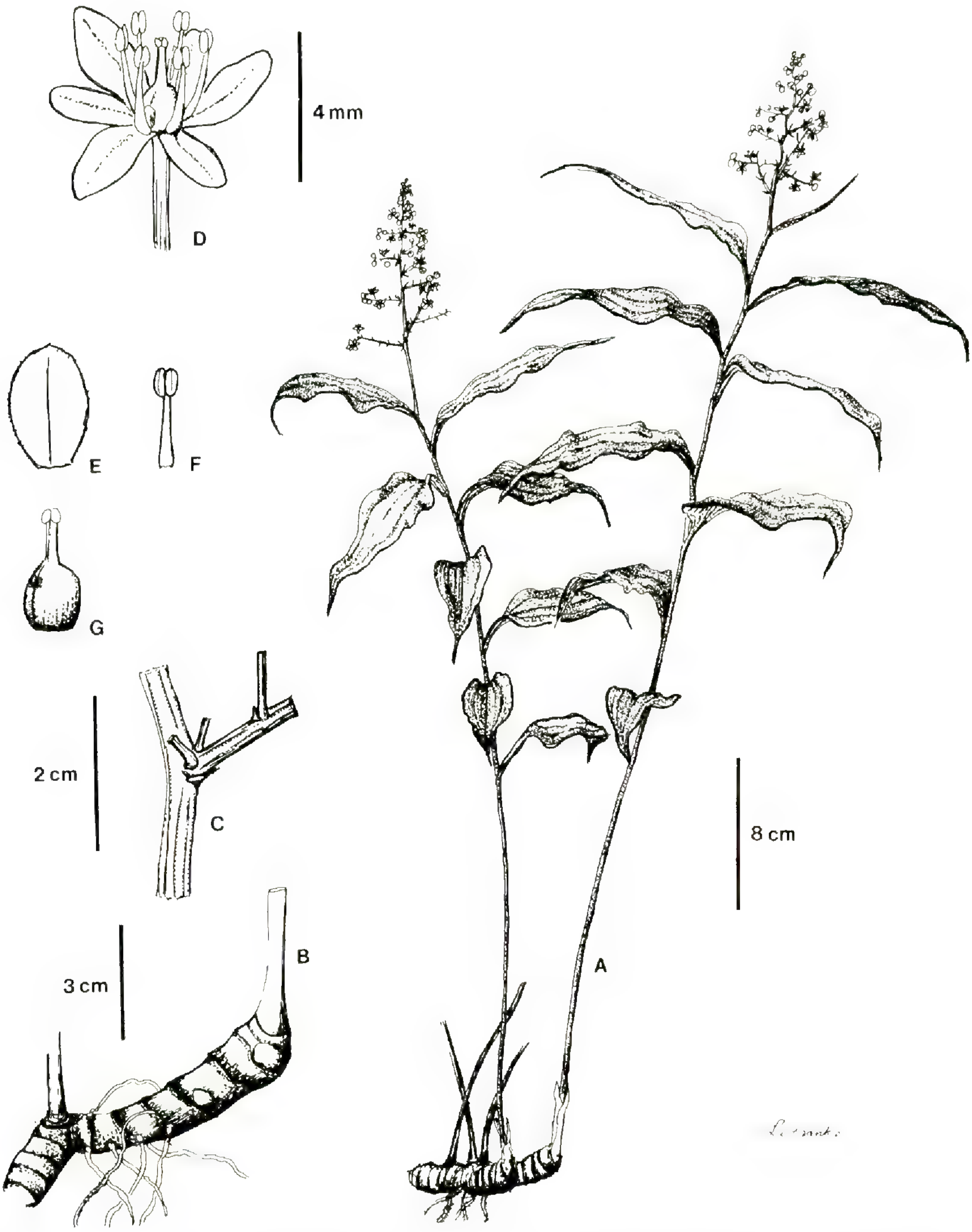


FIGURE 18. *Maianthemum septifolium* (*LaFrankie 84-V-19B,* GH): A, leafy shoots with inflorescences; B, rhizome; C, lateral branch of inflorescence; D, flower; E, tepal; F, stamen; G, gynoecium.

cal, slightly flattened, 2–5.5 by 0.8–1.4 cm, the scale leaves 7 or 8, the internodes 5–8(–12) mm long, shorter apically, the lateral buds 7, axillary, 1 or 2 developing as leafy shoots; epidermis replaced by periderm; starch more dense distally, but nowhere very dense. Leafy stem stiff, upright, tapering, 35–55 cm long, 2.5–3.5 mm wide at base, the surface smooth, glabrous; foliage leaves 6 to 9 (or 10); internodes 3–5 cm long, shorter apically. Leaves with petiole 5–

9 mm long; blade elliptic, 9–14 by 3.5–5(–7) cm, the apex acuminate, the base tapered, the margin slightly undulate, entire or with denticles near apex, the veins ranked, the surfaces glabrous. Inflorescence a cylindrical panicle with 25 to 60 flowers; main axis upright, stiff, slightly flexuate, 6–8 cm long, 1–1.5 mm wide at base, ribbed, green, glabrous; internodes 8 to 12 (to 15), 4–7 mm long; lateral axes racemes (rarely lower ones dense fascicles), arranged in helix, spreading, 10–25 mm long, with 1 or 2 flowers at base and others at intervals of 1–3(–5) mm, with bract subtending each raceme. Flowers trimerous; pedicel 2–4 by 0.8–1.2 mm, ribbed, glabrous, with bract subtending; tepals more or less uniform, 2–4 by 1.2–2 mm, reflexed to spreading, white; stamens inserted at tepal base, the filament 1.2–1.5 mm long, thin, the anther 1–1.2 mm long; ovary spherical, 1.2–1.5 mm in diameter, the style ca. 1 mm long, the stigma distinctly 3-lobed, 0.6 mm broad. Fruits spherical to weakly 3-lobed, 8 mm broad, green with red spots when young, maturing to red; seeds 1 to 3, spherical, 1–1.5 mm in diameter. Chromosome number $2n = 36$ (*fide* M. S. Cave, voucher *Tillet 636-5* (UC)).

TYPE. Mexico, Chiapas, 9 km S of Rayón, 6 km N of Rincón Chamula, steep hillside, cloud forest, 19 May 1984, *LaFrankie 84-V-19B* (holotype, GH).

ECOLOGY AND DISTRIBUTION. Clonal, forming dense clumps along trails, in broken forest, on steep slopes; 1800–2800 m alt. Flowering January–July; fruits maturing slowly, retained 3–6 months; fruiting and flowering stems sometimes occurring on same individual.

Principally in northern highlands of Chiapas, Mexico.

SPECIMENS EXAMINED. **Mexico.** VERACRUZ: Chicoquiaco, *Ventura 7018* (F). CHIAPAS: vic. Pueblo Nuevo Solistahuacán, *Breedlove 19789* (DS), *19842* (DS, F, LL), *20012* (DS), *Clarke 357* (DS), *Lathrop 5209* (DS), *5816* (DS, MO, US), *Thorne 40310* (DS), *41089* (DS), *Tillet 636-5* (DS, GH, US), *Ton 2801* (DS), *2844* (DS, WIS), *Zuill 59* (DS), *193* (DS); vic. Tenejapa, *Breedlove 10806* (DS, F, MICH, MS, NY, US), *Ton 593* (DS, F, MS, NY, US), *1752* (DS, DUKE, NY, US), *2316* (DUKE, WIS); 2 mi S of Jitotol, *Roe et al. 1187* (F, WIS).

In dimensions *Maianthemum septifolium* is intermediate between *M. scilloideum* and *M. paniculatum*. This is another of the species with paniculate inflorescences that was previously confused with *M. paniculatum*, but it can be distinguished from that species by the smaller stature at which it reaches reproductive maturity. *Maianthemum paniculatum* does not initiate an inflorescence until it has at least ten foliage leaves, then continues to produce larger shoots with as many as 17 leaves. Most plants of *M. septifolium* are quite constant in producing shoots with a maximum of seven leaves; only rare collections have as many as ten.

This species is somewhat unusual in the volume of nectar it exudes from the septal nectaries. A large, clear drop of viscid nectar collects at the tepal junction below each septal pore.

Although it is not a widespread species, I have found *Maianthemum septifolium* to be one of the more hardy and one of the easiest to keep in cultivation. It produces shoots more or less continuously and reaches reproductive size very quickly.

14. **Maianthemum stellatum** (L.) Link, Enum. Hort. Berol. Alt. **1:** 343. 1821. FIGURE 19, MAP 9.

Convallaria stellata L. Sp. Pl. 316. 1753; *Tovaria stellata* (L.) Necker ex Baker, J. Linn. Soc., Bot. **14:** 565. 1875; *Smilacina stellata* (L.) Desf. Ann. Mus. Natl. Hist. Nat. **9:** 52. 1807; *Asterantherum vulgare* Kunth, Enum. Pl. **5:** 151. 1821 (nomen illegit.); *Unifolium stellatum* (L.) E. Greene, Bull. Torrey Bot. Club **15:** 287. 1888; *Vagnera stellata* (L.) Morong, Mem. Torrey Bot. Club **5:** 114. 1894; *Asteranthemum stellatum* (L.) Niewl. Amer. Midl. Naturalist **3:** 109. 1913. TYPE: probably described from literature (lectotype, here chosen, Cornut, Canad. Pl. *t. 33.* 1635).

Smilacina stellata var. *uniflora* Pursh, Fl. Amer. Sept. **2:** 733. 1814; *Asteranthemum vulgare* Kunth var. *uniflora* (Pursh) Kunth (nomen illegit.). TYPE: not determined (but see *Sherard Herbarium* no. *725,* OXF).

Vagnera angustifolia Raf. Autik. Bot. 68. 1840. TYPE: United States, near Niagara Falls, *Rafinesque s.n.* (holotype, PH?, probably destroyed; lectotype, here chosen, protologue).

Tovaria sessilifolia Nutt. ex Baker, J. Linn. Soc., Bot. **14:** 566. 1875 (*Smilacina sessilifolia* Nutt. ex Baker, pro syn.); *Unifolium sessilifolium* (Baker) E. Greene, Bull. Torrey Bot. Club **15:** 287. 1888; *Vagnera sessilifolia* (Baker) E. Greene, Man. Bot. San Francisco, 316. 1894; *Smilacina stellata* (L.) Desf. var. *sessilifolia* (Baker) Henderson, Bull. Torrey Bot. Club **27:** 358. 1900. TYPE: United States, Rocky Mtns. and Columbia Woods, [ca. 1835,] *Nuttall s.n.* (lectotype, here chosen, K; isolectotype, PH!).

Unifolium liliaceum E. Greene, Pittonia **1:** 280. 1889; *Vagnera liliacea* (E. Greene) Rydb. Mem. New York Bot. Gard. **1:** 101. 1900; *Smilacina liliacea* (E. Greene) Wynd. Amer. Midl. Naturalist **17:** 902. 1936. TYPE: not determined.

Smilacina stellata (L.) Desf. f. *paniculata* St. John, Proc. Biol. Soc. Wash. **50:** 4. 1937. TYPE: United States, Washington, Silverton, 1899, *Bouck 185,* in part (holotype, WS!).

Vagnera leptopetala Rydb. Bull. Torrey Bot. Club **28:** 268. 1901. TYPE: United States, headwaters of Sangre de Cristo Creek, 1901, *Rydberg & Vreeland 6441* (holotype, NY!).

Vagnera stellata (L.) Morong var. *mollis* Farw. Bull. Torrey Bot. Club **42:** 357. 1915. TYPE: United States, Michigan, Parkdale Farm, 30 May 1914, *Farwell 3651* (holotype, MICH; isotype, GH!).

Smilacina stellata (L.) Desf. var. *crassa* Marie-Vict. Contr. Lab. Bot. Univ. Montréal **14:** 16. 1922. TYPE: Canada, Québec, Île Nue, archipel de Mingan, 29 July 1926, *Victorin & Rolland 24249* (holotype, MT; isotypes, GH!, PH!).

Smilacina stellata (L.) Desf. var. *sylvatica* Marie-Vict. & Rouss. Contr. Lab. Bot. Univ. Montréal **36:** 66. 1940. TYPE: Canada, Québec, Rivière Petite-Cascapédie, 10 April 1930, *Victorin & Rolland 33831* (holotype, MT; isotype, GH!).

Terrestrial herb, 15–45 cm tall. Roots dimorphic, 40 to 150 small ones (0.5–0.7 mm broad) scattered over each rhizome unit, 3 to 6 large ones (0.9–1.2 mm broad) clumped near base of leafy shoot. Rhizome a long-linear sympodium, forking, spreading, the individual units long, narrow-cylindrical, 15–40(–80) cm by 3–4.5 mm, the scale leaves 5 or 6, the 2nd and 3rd internodes 5–25 cm long, others 3–10 mm, the lateral buds 3 or 4, axillary, 2 or 3 developing as leafy shoots; epidermis replaced by densely pilose absorptive layer above distinct hypodermis; starch abundant in rhizome portions 1–2 years old, depleted in older portions. Leafy stem stiff, upright, 25–50 cm long, 2–3.5(–5) mm broad at base, the surface smooth, with denticles; foliage leaves 8 to 11 (to 14); internodes 2–3.5 mm long, shorter apically. Leaves clasping (sometimes

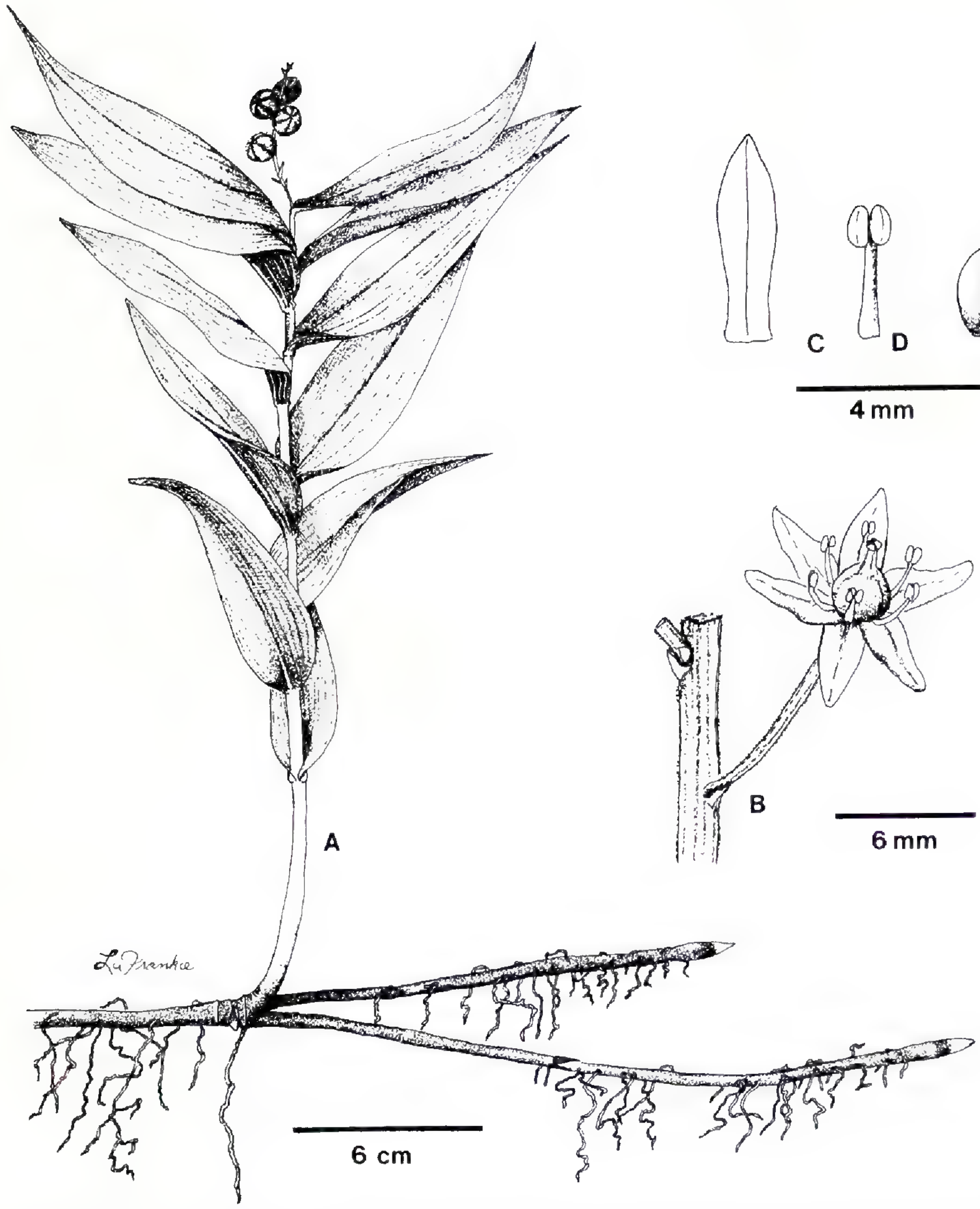
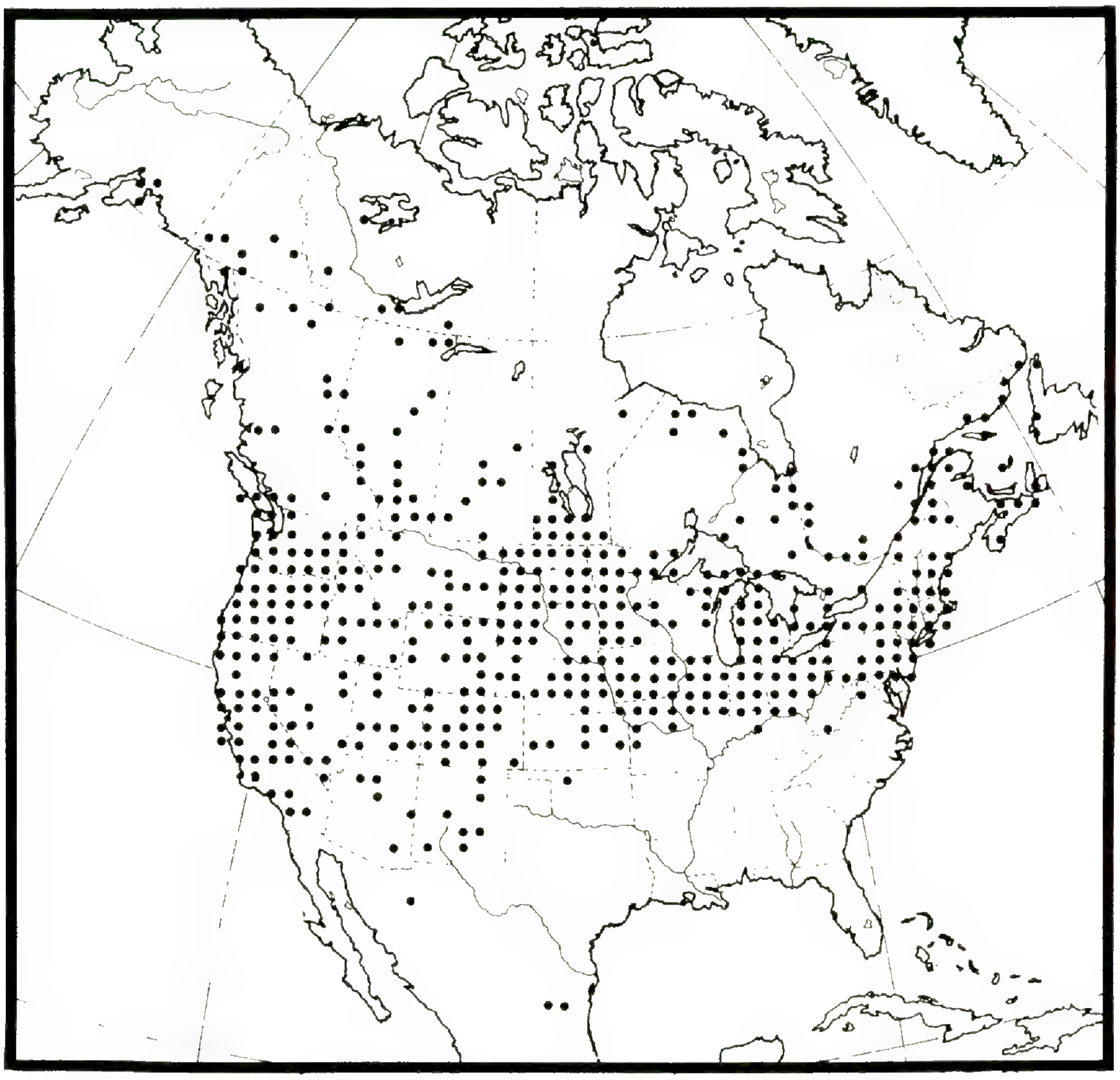


FIGURE 19. *Maianthemum stellatum* (*LaFrankie 76*, GH): A, rhizome, leafy shoot, and infructescence; B, flower; C, tepal; D, stamen; E, gynoecium.

short-petiolate in western United States); blade ovate-elliptic to lanceolate, 5–6(–10) by 2.5–3.5(–5.5) cm, the apex acute, the base rounded, the margin flat, with denticles very distinct and pointed forward, the veins of uniform strength or weakly ranked, the surfaces usually pubescent. Inflorescence a simple raceme with 6 to 15 flowers; main axis upright, straight or slightly flexuous, 4–5.5 cm long, 0.5–1.5 mm broad at base, ribbed, green, pubescent; internodes 3–8 mm long; flowers arranged in helix. Flowers trimerous; pedicel arched-ascending, ribbed, usually pubescent or denticulate, with 1 bract subtending, usually an additional 1 at pedicel base or at midlength; tepals uniform, spreading, 4–5 by 1.5–2 mm, white; stamens inserted at tepal base, the filament 1.2–1.5 mm long, thin, the anther 0.6–0.8 mm long; ovary spherical to cylindrical, ca. 1



MAP 9. Distribution of *Maianthemum stellatum*.

mm broad, style 1.3–1.8 mm long, stigma obscurely 3-lobed. Fruits spherical, 4–6 mm in diameter, green with black stripe along each median carpel vein when young, maturing to red; seeds 1 to 6, spherical, 2.5–3 mm in diameter. Chromosome number $2n = 36$ (Kawano & Iltis, 1966).

ECOLOGY AND DISTRIBUTION. Clonal, with scattered occurrence throughout much of range, although in some habitats abundant to subdominant; generally in wet sites with periodic edaphic disturbance. Flowering April–June; fruits retained through September.

Very common in sand dunes of Atlantic coast from New Brunswick to New Jersey, inland along river shores, creek banks, sand dunes, gravel and sand washes of prairies; in American Midwest and Far West more frequently in marginal woodland habitats and oak-pine openings, especially above 1000 m.

Eastern limit extending from Newfoundland (Northumberland Co., Fox Is., *Blake 5687* (LL)) and Nova Scotia (Cape Breton Is., Bird Is., *Nichols 588* (GH)) south along coast through New Jersey (Cape May Co., 1 mi S of Peermont, *Fender 1369* (GH)). Inland, southern limit occurring through mountains of

Virginia (Giles Co., along Rte. 100, ca. 10 mi S of Pearisburg, *Nicely s.n.,* 19 May 1961 (WVA)) and West Virginia (Summers Co., river bank near Bellpoint, *Boone 194* (WVA)) west through single location in Kentucky (Lewis Co., along Chalk Ridge Road, ca. 6 mi N of Tollesboro, *Thieret 53617* (KNK)), through Posey Co., Indiana (Deam, 1940), and Illinois (Monard Co., *E. Hall s.n.* (PH); Wabash Co. (Mohlenbrock & Ladd, 1978)) to Missouri (Shelby Co., Shelbina, *Palmer 40852* (GH); Shannon Co. (Steyermark, 1963)) and Oklahoma (Woodward Co., Boiling Springs State Park, *Goodman 7303* (GH)). Northern limit extending from Québec (S shore James Bay, Île Lemoine, *Dutilly 14-083* (GH)) to Manitoba (Hayes R., opposite mouth of Fox R., *Scoggan 5859* (GH)) to Northwest Territories (MacKenzie Distr., Salt Plain, W of Fort Smith, *Cody 3788* (LL)) and Yukon Territory (Whitehorse, *Calder 2863* (CAS); Ross R., Pelly R., upper terrace, *Denniston 25* (WIS)). In West, exhibiting remarkable latitudinal range, from Alaska (Chugach Mtns., middle slope, near Lake Eklutna, *York B205* (LL)) south through Rocky Mtns. and California ranges, here occurring at both low (San Mateo Co., San Andreas Lake, ca. 200 m, *Baker 1915* (GH, LL)) and high (Mono Co., Harvey Monroe Hall Natural Area, 3230 m, *Clausen 1636* (UC)) elevations, south to southern California (Riverside Co., San Gabriel Mtns., Strawberry Valley, *Grant s.n.* (CAS); Los Angeles Co., San Gabriel Mtns., Dawson Saddle, *Griesel s.n.* (DS)) and through Southwest to Nevada (Clark Co., Charleston Park, *Clokey 7879* (CAS, GH, US, WIS) and northern Mexico (Chihuahua, near Colonia Garcia in Sierra Madre, 7500 ft, *Townsend & Barber 35* (F, MO, NY, UC, US)), widely disjunct in highest peaks of Nuevo León (Municipio Galeana, Cerro Potosí, shelter of thickets below timberline, 11,700 ft, *Schneider 1033* (F)). Specimen from Sweden (*F. Ahlberg s.n.,* ca. 1869 (US)) probably escaped from cultivation.

Maianthemum stellatum is the only species of the Linnaean genus *Convallaria* without a type at LINN. Specimens annotated "*C. stellata*" in other Linnaean depositories are of material evidently annotated after 1753. Linnaeus made no mention of *M. stellatum* prior to his description in *Species Plantarum,* although it had been cultivated in England and Europe since the early seventeenth century (Aiton, 1814), and he most likely had seen it at one time or another. In *Species Plantarum* Linnaeus cited published illustrations of *M. stellatum* found in Morison (1699) and Cornut (1635) and probably based his description on these. The illustrations in Morison are copies of the earlier illustrations in Cornut, so I have chosen Cornut's most representative illustration as the lectotype.

My treatment of *Maianthemum stellatum* is similar to that of Galway (1945) in that I find no basis to maintain any taxonomic rank for any of the variants found in the western United States. In California and Oregon *M. stellatum* exhibits considerable diversity of form, especially in leaf outline, and botanists in the region have occasionally recognized one or more varieties or species within this range. Greene, in particular, thought that there were two very definite species in the upper and lower Sierras, distinguished chiefly by subtle differences in leaf coloration, indumentum, and fruit color. Only fruit coloration could be of significance, but Greene based his observations on herbarium

specimens, which are quite unreliable with regard to color constancy. Plants from Oregon and California generally have longer pedicels than do individuals from more eastern states, but this feature is not correlated with any other, and the range of pedicel length is large even in the West. Considering the very broad distribution of this species, it is somewhat surprising that more variation is not exhibited. Three distinctive features (extended rhizome, dimorphic roots, and striping on immature berries) are evidently constant throughout the entire range. The singularity of these features and the constancy of their occurrence further support the recognition of a single broadly distributed species.

15. **Maianthemum trifolium** (L.) Sloboda, Rostlinnictví, 192. 1852 (*fide* Holub, 1974). FIGURE 20, MAP 10.

Convallaria trifolia L. Sp. Pl. 316. 1753; *Smilacina trifolia* (L.) Desf. Ann. Mus. Natl. Hist. Nat. **9:** 52. 1807; *Asteranthemum trifoliatum* (L.) Kunth, Enum. Pl. **5:** 153. 1850; *Tovaria trifolia* (L.) Necker ex Baker, J. Linn. Soc., Bot. **14:** 565. 1875; *Unifolium trifolium* (L.) E. Greene, Bull. Torrey Bot. Club **15:** 287. 1888; *Vagnera trifolia* (L.) Morong, Mem. Torrey Bot. Club **5:** 114. 1894; *Asteranthemum trifolium* (L.) Niewl. Amer. Midl. Naturalist **3:** 109. 1913. TYPE: [Soviet Union, Siberia?, 1740–1750?] (lectotype, here chosen, LINN 436.6).

Vagnera pumila Standley, Smithsonian Misc. Collect. **56**(33): 1. 1912. TYPE: Canada, Alberta, Prairie Creek, 3 July 1911, *Riley 100* (holotype, US (US no. *622636!*); isotype, US (US no. *690417!*)).

Vagnera trifolia (L.) Desf. f. *bifolia* Farw. Bull. Torrey Bot. Club **42:** 358. 1915. TYPE: United States, Michigan, Keweenaw Peninsula, 16 July 1886, *Farwell 3782, pro parte* (holotype, MICH).

Vagnera trifolia (L.) Desf. f. *unifolia* Farw. Bull. Torrey Bot. Club **42:** 358. 1915. TYPE: United States, Michigan, Keweenaw Peninsula, 16 July 1886, *Farwell 3782, pro parte* (holotype, MICH).

Aquatic herb, 4–15 cm tall. Roots uniform, 2 per node, 10–30 cm by 0.5–1 mm. Rhizome an irregularly branched sympodium, the individual units cylindrical, 2–30 cm by 1–2 mm, the scale leaves 3 to 10, the internodes 1–50 mm long, shorter apically, the lateral buds 1 at every node, axillary, 1 to 4 (to 8) forming renewal shoots; epidermis persistent; starch found only near rhizome apex. Leafy stem upright, 10–25 cm long, 2–3 mm broad at base, lower portion usually submersed, the surface smooth, glabrous; foliage leaves 2 to 4; internodes 3–6 cm long. Leaves clasping, sessile; blade elliptic, 5–12 by 2.5–4 cm (rarely 1 by 3 cm), the apex acute to acuminate, the base narrowly tapering to subpetiolate, the margin flat, with denticles distinct, the veins of uniform strength or weakly ranked, the surfaces glabrous. Inflorescence a simple raceme with 5 to 15 flowers; main axis upright, stiff, straight, 4–7 cm long, 1–2 mm wide at base, round or sometimes flattened, smooth, green, glabrous; internodes 5 to 15, 3–6 mm long, flowers arranged in helix. Flowers trimerous; pedicel spreading to arched-ascending, 1–3 by 0.5 mm, smooth, glabrous, with 1 bract subtending, additional 1 at right angles to first and either at pedicel base or midpoint; tepals uniform, spreading, 2.5–4 by 1.5–2 mm, white; stamens inserted at tepal base, the filament 1.5–2 mm long, thin, the anther 0.5–0.7 mm long; ovary spherical or cylindrical, 2–2.5 by 1.5–2.4 mm, the style 0.5–1.5 mm long, the stigma distinctively 3-lobed, 0.6 mm broad. Fruits spher-

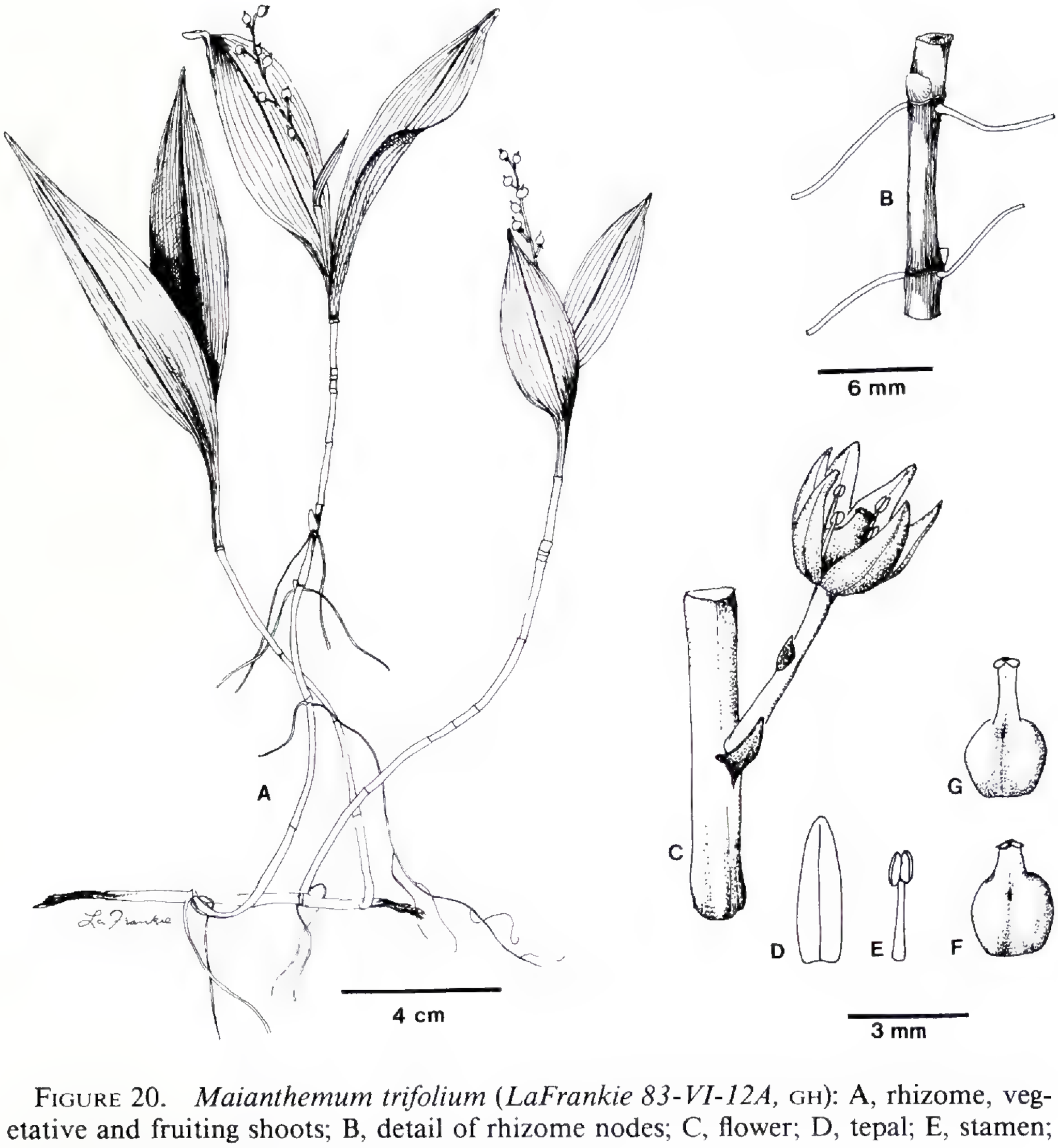
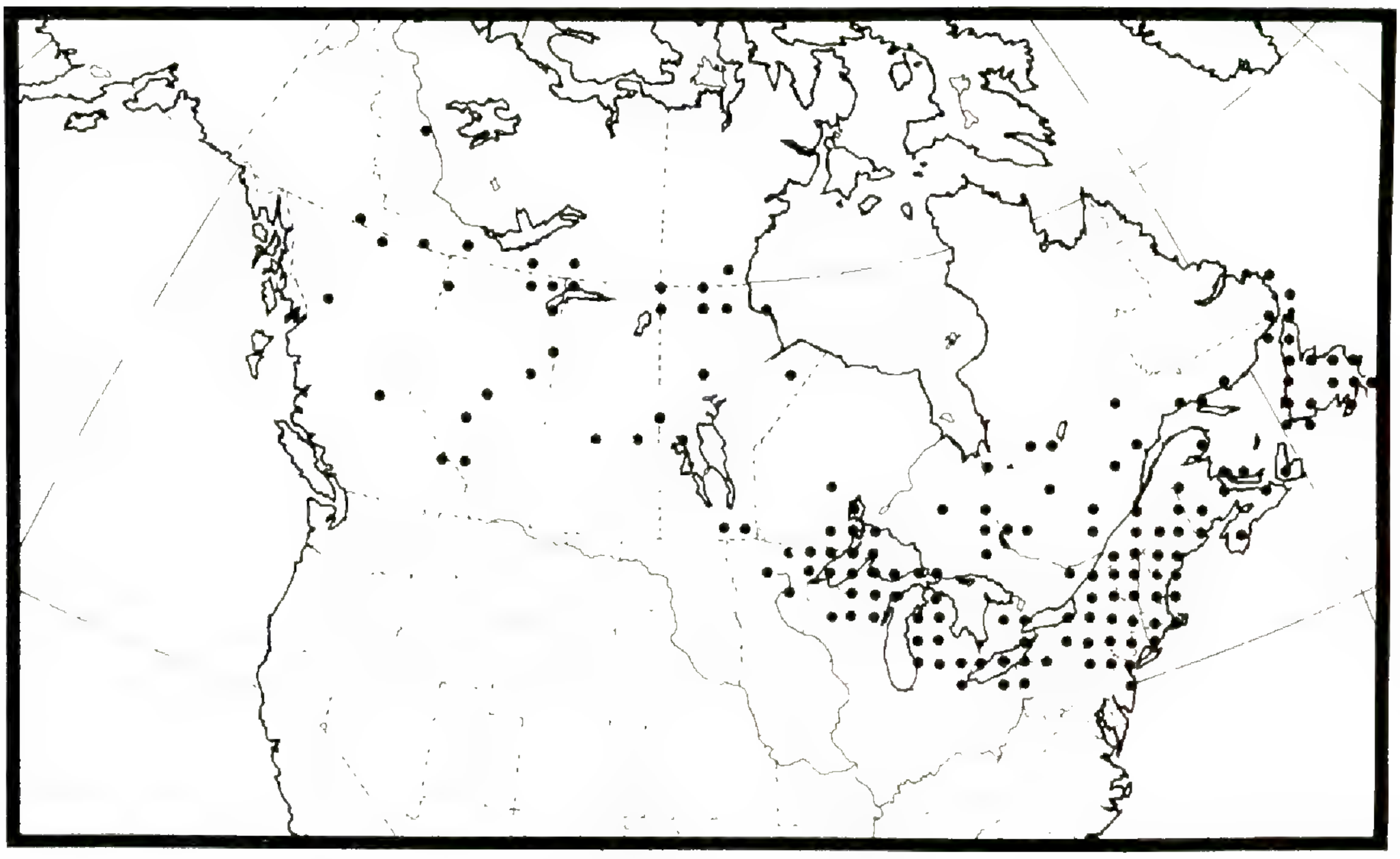


FIGURE 20. *Maianthemum trifolium* (*LaFrankie 83-VI-12A*, GH): A, rhizome, vegetative and fruiting shoots; B, detail of rhizome nodes; C, flower; D, tepal; E, stamen; F, G, gynoecia, showing variation in style length.

ical, 4–6 mm in diameter, green when young, maturing to red; seeds up to 3, spherical, 2 mm in diameter. Chromosome number $2n = 36$ (Kawano & Iltis, 1966).

ECOLOGY AND DISTRIBUTION. Clonal; sphagnum bogs, muskegs, and wet forests; sea level to 1000 m alt. Flowering May–June; fruits retained through August or September.

Eastern limit extending from Labrador (Salmon Bight, 53°27′N, 55°47′W, *Porsild 24* (GH); Brig Bay, *Fernald 26518* (GH, PH)) to New Jersey (Sussex Co., Pine Swamp, *Griscom 12041* (GH); Morris Co., Budd's Lake, *Heritage s.n.* (PH)). Southern limit extending through Pennsylvania (Monroe Co., sphagnum bog, 1 mi N of Tobyhanna, *Buser 11562* (GH); Bedford Co. (Wherry *et al.*, 1979)), northern Ohio (Lorain, Cuyahoga, and Fulton counties—Braun, 1967), and southern Michigan (Kalamazoo and Washtenaw counties—Voss, 1972).



MAP 10. Distribution of *Maianthemum trifolium*.

Very common but infrequently collected in wet forests and bogs of lower Ontario. Northern limit extending through northern Ontario (Obijawa Provincial Park, near Siouk, *Anderson s.n.* (WIS)) to northern Manitoba (vic. Churchill, *Schofield 6571* (WTU)) and west through Mackenzie Basin (Lake Athabasca, Shelter Point, 58°50′N, 110°50′W, *Raup 433* (GH)); rare in northern Alberta (2 mi SW of Fort Smith, Northwest Territories, 60°00′N, 111°53′W, *Cody 4021* (GH, WTU)) and Yukon Territory (E end of Watson Lake, ca. 60°05′N, 128°43′W, *Raup 11058* (GH)). Western limit in British Columbia (Germansen Landing of Omineca R., *McCabe 7732* (WTU); mi 370, Alaska Highway, *Szczawinski s.n.* (WTU)). Evidently absent from northwestern continental U. S. and Alaska but reappearing in Siberia and northern China.

Although *Maianthemum trifolium* is chiefly distributed in North America, Linnaeus knew the species only from eastern Asia. There are two specimens at LINN. Number *436.6* is a plant with three leaves, annotated "Convallaria trifolia 7" by Linnaeus and bearing the note "Phallangium forte 5 Amm. Siberia" on the back. Number *436.7* is a smaller plant with two leaves and a young infructescence, annotated "Convallaria trifolia" and bearing the symbol that indicates its origin in Kamchatka. I have chosen number *436.6* as the lectotype because the protologue describes the species as having three leaves, not two, and the origin is described as "Siberiae sylvis," not Kamchatka. This specimen undoubtedly came from one of Linnaeus's sources in Russia between 1740 and 1755, but I can find no published account concerning its origin. Although the note on the back of the specimen mentions J. Amman ("Amm."), we cannot assume it to be one of his collections because the idea of the plant growing in "sylvis" is directly from Gmelin (1747). Therefore, it is likely that Linnaeus wrote the diagnosis using both the published descriptions of Amman (1739) and Gmelin and specimen *436.6*.

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A TAXONOMIC REVISION OF CRAIBIODENDRON (ERICACEAE)[1,2]

WALTER S. JUDD[3]

The genus *Craibiodendron* W. W. Smith (including *Nuihonia* Dop) contains five species and is limited to southeastern Asia. It is closely related to several genera in the Andromedeae (Ericaceae) such as *Lyonia* Nutt., *Agarista* D. Don, and *Pieris* D. Don (Stevens, 1970; Judd, 1979). The group has not been revised prior to the present work. In this paper I have therefore reevaluated the limits of the genus and revised the species; nearly 300 herbarium specimens have been examined. I have attempted to employ consistent specific delimitations, compare the taxa, interpret their phylogenetic relationships, and develop descriptions and practical keys for identification.

GENERIC RELATIONSHIPS

The small genus *Craibiodendron* (Ericaceae subfam. Vaccinioideae tribe Andromedeae) was first described by W. W. Smith (1911), who then suggested that it was related to *Lyonia* and *Pieris*. In the major paper dealing with the genus prior to the present work, Smith (1912) altered his opinion and considered *Craibiodendron* to be more closely related to *Leucothoë* D. Don on the basis of its imbricate, almost free sepals, muticous anthers, and winged seeds. In 1961 Lems (note on *Henry 13137*, NY) suggested, possibly on the basis of inflorescence structure, that *Craibiodendron* is "near-ancestral" to *Pieris*. Dop (1930) segregated the very similar genus *Nuihonia* on the basis of its supposedly arillate seeds. The relationships of *Nuihonia* and other genera of Andromedeae to *Craibiodendron* are discussed briefly below.

Generic relationships within the Andromedeae have been studied by Stevens (1970, 1971) and Judd (1979), and the genera *Craibiodendron, Lyonia, Agarista, Pieris,* and *Leucothoë* are compared in TABLE 1. *Craibiodendron* is phenetically distinctive within the Andromedeae and is characterized by its often *superposed buds*[4] with two (to four) bud scales and a rather elongated attachment to the twig; twigs with a homogeneous pith; petiole and leaf midrib with bifacial vascular bundles; indumentum of biseriate-stalked, small-headed, multicel-

[1]The fourth in a series of revisionary studies of genera of the Andromedeae (Ericaceae). Previously studied genera include *Lyonia* (Judd, 1981), *Pieris* (Judd, 1982), and *Agarista* (Judd, 1984).

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[4]Characters in italics are unique within the *Lyonia* group of the Andromedeae.

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lular hairs; axillary *panicle- to racemelike cymose inflorescences with terminal flowers* that "overwinter" within the bud; clearly imbricate calyx lobes; *often campanulate* and carnose *corollas*; papillose and geniculate filaments lacking spurs or awns; and *large, thick-walled capsules bearing a few large seeds, each with a prominent unilateral wing* (see also Judd, 1979). The species of *Craibiodendron* are also distinctive in having spherical to polygonal parenchymatous cells at the vein endings in the leaves (T. A. Rao, pers. comm.; Rao & Chakraborti, 1982). The genus is phenetically closest to *Agarista* (including *Agauria* (DC.) J. D. Hooker) and *Leucothoë* but shows differences from these genera that are of "generic magnitude" (Judd, 1979, *fig. 1, table 2*). *Nuihonia* (*N. sclerantha* Dop) consistently differs from *C. kwangtungense* S. Y. Hu only in having abaxially unicellular-pubescent calyx lobes; its seeds are not arillate. The genus *Nuihonia* is therefore not recognized.

Cladistically, *Craibiodendron* is most closely related to *Lyonia*. They are linked by the following synapomorphies (i.e., shared derived characters): biseriate-stalked gland-headed hairs, bifacial midrib bundles, and buds with usually two scales (the last feature, however, has undergone a reversal in *Lyonia* sect. *Maria*). *Craibiodendron* shows the autapomorphic character states of large, unilaterally winged seeds, robust capsules, and superposed buds, while the four sections of *Lyonia* are linked by the derived character states of glandular hairs with large swollen heads, bracteoles basal or nearly so, staminal spurs with disintegration tissue, and capsules with thickened sutures that often separate from the valves during dehiscence (see Judd, 1979). The presumed monophyletic group consisting of *Lyonia* and *Craibiodendron* is in turn linked with *Agarista* by the presence of geniculate filaments, and all of these are eventually linked with *Pieris* in having bands of fibers in the phloem, filament spurs (presumably lost in *Craibiodendron, Agarista,* and some species of *Lyonia*), and elongate testa cells (lost in some species of *Pieris*). This group of four genera also has anomocytic stomata, awnless stamens, and a chromosome number of $x = 12$; it shows a strong tendency for epidermal lignification (Judd, 1979). Stevens (1970) and Judd (1979) refer to these genera as the "*Lyonia* group." In contrast, *Leucothoë* is cladistically isolated from these genera due to its paracytic stomata, often awned stamens, and chromosome number of $x = 11$ (Judd, 1979). *Leucothoë* is probably closer to *Zenobia* D. Don, *Gaultheria* L., *Pernettya* Gaudich., and relatives—the "*Gaultheria* group" of Stevens (1970) and Judd (1979).

It is evident from TABLE 1 and from the investigations of Stevens (1970) and Judd (1979, both phenetic and cladistic analyses) that *Craibiodendron* is more closely related to *Lyonia* and associated genera than it is to *Leucothoë,* thus supporting W. W. Smith's (1911) suggested affinities. When the characters used by Smith (1912) to indicate relationship with *Leucothoë* are analyzed, this conclusion becomes even clearer. The imbricate calyx lobes shared by *Leucothoë* and *Craibiodendron* are a symplesiomorphy and are thus not indicative of cladistic relationship. The unilaterally winged seeds of *Craibiodendron* are not comparable to those of some species of *Leucothoë* in which the wing is formed from numerous individual cells with fringed outer walls. The winged seeds of these two genera have evolved independently and do not

TABLE 1. **Variation in selected morphological and anatomical characters in Craibiodendron and related genera.**

CHARACTER	TAXON				
	Craibiodendron	**Lyonia**	**Agarista**	**Pieris**	**Leucothoë**
Phloem with bands of fibers	+	+	+	+	−
Glandular hairs biseriate stalked	+	+	−	+	−
Leaves					
Margin entire	+	+/−	+ (−)	+/−	−
Midrib bundle bifacial	+	+ (−)	−	− (+)	−
Stomata anomocytic	+	+	+	+	−
Epidermis lignified	+	+/−	+	+/−	−
Inflorescences "overwintering" in bud	+	+	+	−	−
Calyx lobes imbricate	+	+/−	+	−	+
Stamens					
Filaments lacking spurs	+	+/−	+	−	+
Filaments geniculate	+	+	+	− (+)	−
Anthers lacking awns	+	+	+	+	− (+)
Seeds					
Winged	+ (unilateral)	−	−	− (+, 2 slight wings)	−/+ (bulging cells)
Testa cells elongate	+	+	+	+/−	−

indicate close phylogenetic relationship. Finally, the stamens of *Craibiodendron* and *Leucothoë,* although similar in lacking spurs, are very different. Those of *Craibiodendron* lack appendages and have slender, geniculate filaments, while those of *Leucothoë* have awns and stout, more or less straight filaments. The morphology of the stamens indicates a closer relationship of *Craibiodendron* to *Lyonia* or *Agarista* than to *Leucothoë.*

CLADISTIC ANALYSIS

The phylogenetic relationships of the species of *Craibiodendron* were investigated using two methods: the manual Wagner Groundplan Divergence Method (Wagner, 1962, 1980); and the computer programs WAGNER, MIX (using Wagner Network Parsimony Method; described in Kluge & Farris, 1969), and PENNY (using "branch and bound" algorithm; see Hendy & Penny, 1982), which were developed by J. Felsenstein and are part of his PHYLIP package (Felsenstein, 1984). Twelve characters were used and assigned primitive (plesiomorphic) and advanced (apomorphic) states (see TABLE 2). For all characters except one a taxon was scored 0 if primitive and 1 if advanced. For character G, length of corolla lobes in comparison to length of tube, which is composed of a three-state transformation series (see TABLE 3), the most advanced state was assigned a value of 2 in the Wagner Groundplan Divergence Method; in

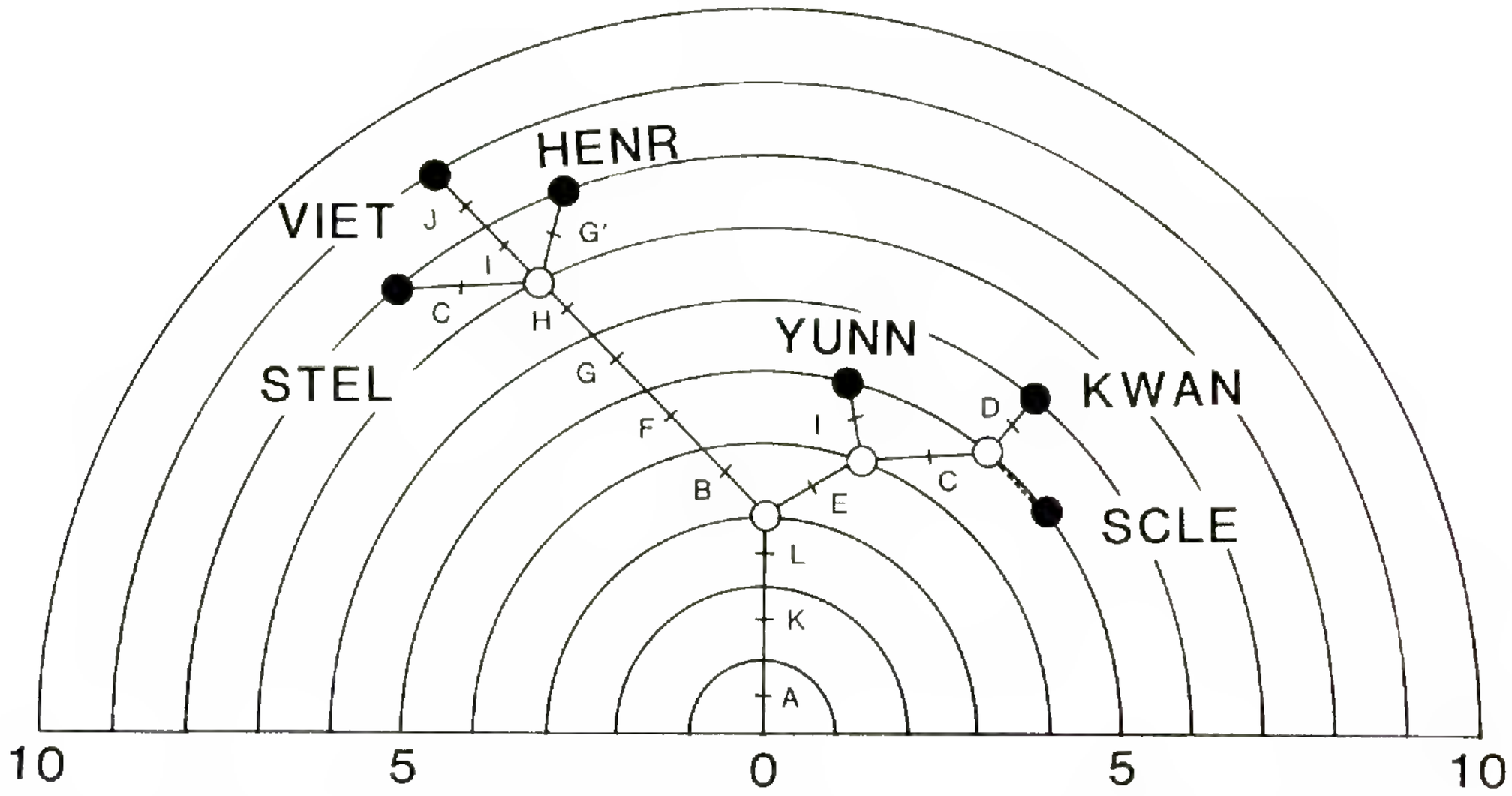


FIGURE 1. Wagner Tree for species of *Craibiodendron*: extant taxa (black circles); hypothetical ancestors showing only derived character states shared by taxa positioned distally on tree (open circles). Synapomorphies indicated on cladogram; taxon names abbreviated by first four letters of specific or varietal epithet.

the WAGNER, MIX, and PENNY computer programs the two advanced states of this character were both assigned a value of 1. TABLE 3 shows all taxa and their character-state values. For each taxon the total divergence index was determined by adding the individual character-state values. In the Wagner Groundplan Divergence Method an attempt was made to construct the shortest tree by hand, minimizing the number of both character-state reversals and parallelisms. The taxa were then plotted graphically (FIGURE 1), with the branching points determined by the mutual groupings of advanced characters and the distance by the divergence of each taxon. The computerized WAGNER, MIX, and PENNY programs also minimize the total number of character-state changes in the construction of the tree. The computer-generated trees were rooted by using a hypothetical ancestor with all plesiomorphic characters (in WAGNER) or by specifying the ancestral character states (in MIX and PENNY).

Cladistic methods require numerous assumptions concerning which is the apomorphic and which the plesiomorphic state of each character. The problems and sources of error associated with the determination of character polarity have been discussed by Stevens (1980, 1981), Crisci and Stuessy (1980), Wheeler (1981), Wiley (1981), Watrous and Wheeler (1981), Donoghue and Cantino (1984), and Maddison, Donoghue, and Maddison (1984). The consensus is that out-group analysis is the most powerful method for determining polarity; the derived states of all characters except D and E (TABLE 2) were determined by out-group comparisons (using the genera *Lyonia, Agarista,* and *Pieris,* successively, as out-groups; see Judd, 1979). For characters D and E, complex cymose (= monotelic) inflorescences were considered to be primitive in comparison with racemose (= polytelic) ones, following the analysis of Weberling (1965). This polarity decision results in a hypothesized loss of terminal flowers

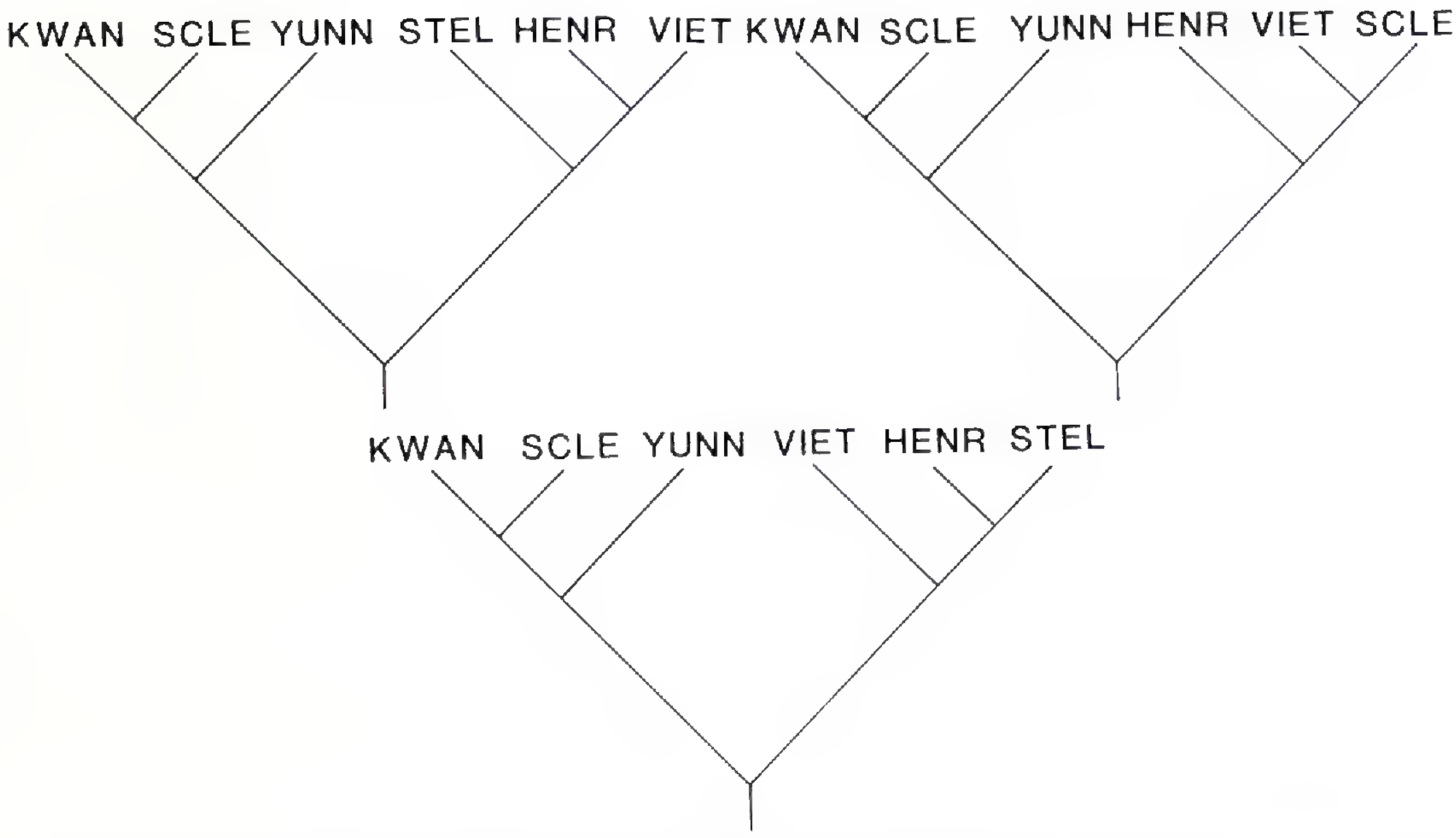


FIGURE 2. Wagner trees generated by PHYLIP programs; all require 15 steps. Taxon names abbreviated by first four letters of specific or varietal epithet.

(and the evolution of racemes) independently within *Agarista, Lyonia,* and *Pieris.* This may indeed have occurred, since a few species of *Agarista* (e.g., *A. pulchella* Cham. ex G. Don and *A. populifolia* (Lam.) Judd) develop inflorescences with some terminal flowers (i.e., partly monotelic), and the detailed studies of Troll (1964) have shown that cymose inflorescences are generally primitive within the Angiospermae. It is noteworthy that Lems (note on *Henry 13137,* NY, 1961) also considered the inflorescence structure (as well as the leaf venation) of *Craibiodendron* to be very primitive in the Andromedeae. However, out-group analysis leads to a reversed polarity decision for these characters; thus groupings based upon them may be suspect. The variation in inflorescence structure within the "*Lyonia* group" of the Andromedeae is indicated in FIGURE 3.

The Wagner trees (or cladograms) resulting from the above procedures (FIGURES 1, 2) indicate that the species of *Craibiodendron* may belong to two phyletic groups: the *C. scleranthum* group (including *C. scleranthum* and *C. yunnanense*) and the *C. stellatum* group (including *C. stellatum, C. vietnamense,* and *C. henryi*). The *C. scleranthum* group is characterized by reduced inflorescences with the secondary axes bearing from one to only ca. six flowers (E). These two species also have glabrous, urceolate to cylindrical corollas with small lobes, and stamens with long (i.e., 2.5–4 mm) filaments. This group might be paraphyletic (if polarity of character E were reversed). Members of the *C. stellatum* group are characterized by campanulate corollas (F) with large lobes (G) that are often unicellular-pubescent (H). The leaves of this group often show impressed secondary and/or tertiary veins (B). The filaments of these species are typically shorter (i.e., 1.5–2.7 mm) than those of the *C. scleranthum* group.

Both groups share the derived character states of often-superposed buds (A),

robust capsules (K), and large, unilaterally winged seeds (L). They are very similar in vegetative and fruit characters, being best distinguished by floral features (see key). *Craibiodendron yunnanense* and *C. scleranthum* are likely the most phenetically primitive extant members of the genus.

The trees resulting from the Wagner Groundplan Divergence Method and Felsenstein's WAGNER, MIX, and PENNY computer programs scarcely differ, which is not unexpected in this small and relatively simple data set; all shortest trees are the same length (15 steps). The only differences are in the resolution of the trichotomy (in the Wagner Groundplan Divergence tree) involving taxa of the *Craibiodendron stellatum* group (see FIGURES 1 and 2). These minor differences probably result from the fact that the procedure that prints out the trees and the internal data structures used in the PHYLIP package of computer programs cannot handle trichotomies. Therefore, trichotomies are expressed as a series of dichotomies, with some branches of zero length (see PHYLIP documentation—Felsenstein, 1984).

DISTRIBUTION

All five species of *Craibiodendron* are limited to southeastern Asia (southern China, eastern India, Burma, Laos, Thailand, Cambodia, and Vietnam), and the group is basically montane, extending from ca. 200 to 3200 m altitude. The center of diversity is in southeastern Yunnan (China), where three species occur. *Craibiodendron stellatum* is the most widely distributed species (see MAP 3), while *C. vietnamense* and *C. scleranthum* var. *scleranthum* are both endemic to very small areas in southern Vietnam (see MAPS 1, 2). The species of *Craibiodendron* tend to be allopatric or only marginally sympatric.

It is of interest that several taxa show strange disjunct distribution patterns. *Craibiodendron stellatum* occurs commonly from southern Yunnan and adjacent Burma to northern Thailand and has scattered disjunct populations southward, extending to the Bi-Doup region of southern Vietnam (MAP 3). A similar disjunction is seen between the northern *C. henryi* and its close relative *C. vietnamense,* the latter also limited to the Bi-Doup region. Finally, in the *C. scleranthum* group, *C. scleranthum* var. *kwangtungense* and *C. yunnanense* are distributed in southern China and adjacent Burma, while *C. scleranthum* var. *scleranthum* has only been collected in southern Vietnam (near Nha-trang). A similar north–south disjunction pattern is seen in *Lyonia,* where *L. ovalifolia* (Wallich) Drude var. *rubrovenia* (Merr.) Judd occurs in both Hainan and southern Vietnam (Judd, 1981). These southern disjunct localities may represent relict populations—indicating a southward displacement of species ranges (during the Pleistocene) relative to their present positions.

TAXONOMIC CRITERIA

Entities that have no major internal morphological discontinuities and show separation from other similar entities by consistent morphological gaps are considered to be species. Species of *Craibiodendron* frequently are distinguished by floral morphology, inflorescence structure, and leaf shape and apex. Such entities have definite geographic distributions and ecological preferences. All

TABLE 2. **Characters used in the cladistic analyses of the species and varieties of Craibiodendron.**

CODE	CHARACTER	PRIMITIVE STATE	ADVANCED STATE
A	Buds	1 per node	Often superposed, 2 or 3 per node
B	Adaxial leaf venation	2° veins not impressed	2° and/or 3° veins at least sometimes impressed
C	Leaf apex	Acuminate or long-acuminate	Acute to rounded or retuse
D	Inflorescence structure	2° and sometimes 3° axes present (panicle-like)	Only 1° axes present (racemelike)
E	2° inflorescence axes	With 7 to 30 flowers	With 1 to 6 flowers
F	Corolla shape	Urceolate or cylindrical	Campanulate
G	Corolla lobes	Small (much less than ½ length of tube)	1: large (ca. ½ length of tube) 2: very conspicuous (much longer than tube)
H	Corolla pubescence	Glabrous	At least sometimes sparsely to moderately pubescent
I	Corolla epidermal cells	± smooth to slightly bulging	Usually papillose
J	Style	Glabrous	Unicellular-pubescent
K	Capsule	Small to moderate-sized	Robust
L	Seeds	Not winged	Unilaterally winged

are rather widespread (see MAPS 1–3) except for *C. vietnamense,* which is limited to a small area of southern Vietnam. Most species appear to be only marginally sympatric. *Craibiodendron stellatum* and *C. vietnamense,* however, both occur in the Bi-Doup area of Vietnam, and there is some distributional overlap in southern Yunnan. The marginally sympatric *C. stellatum* and *C. henryi* differ somewhat in elevational range, with the former occurring from ca. 200 to 1950 m and the latter from 1500 to 2850 m altitude. There may be occasional hybridization when species occur together—for example, in southern Yunnan between *C. stellatum* and *C. henryi* (see discussion under *C. henryi*).

The taxonomic usefulness of (and the variation within) the characters differing within the genus are discussed below. Characters most useful in species delimitation include corolla shape, size, color, and indumentum; leaf shape and apex type; inflorescence structure (number of branch orders, size, number of flowers per secondary axis); capsule and seed size; calyx size and indumentum; and filament length.

HABIT

The habit of species of *Craibiodendron* is quite variable. Depending upon habitat, plants of each species can grow as small shrubs or moderate-sized (to 10–20 m tall) trees. The bark is consistently gray and longitudinally furrowed.

As in the other members of the Andromedeae (see Lems, 1962; Judd, 1981, 1982, 1984), the shoot meristem in *Craibiodendron* has a limited life span, and growth in height is achieved by a succession of equivalent, axillary, orthotropic shoots. All species show a slight variation of Leeuwenberg's model of growth (see Hallé, Oldeman, & Tomlinson, 1978, for description). Floral buds are produced in the leaf axils of the distal portion of the shoots, and the shoot apex aborts. The inflorescences overwinter within the buds, with meiosis presumably occurring in the spring.

The branches vary from terete to slightly angled, and the pith is homogeneous (Stevens, 1971).

INDUMENTUM

The indumentum of *Craibiodendron* is of three distinct types: unicellular hairs; multicellular, biseriate-stalked hairs with small glandular heads; and papillae. The distribution of glandular hairs is too uniform to be of taxonomic value within the genus. However, the distribution and density of unicellular hairs are often taxonomically significant. For example, the pubescence of the abaxial surface of the calyx lobes allows the differentiation of two geographically isolated varieties of *C. scleranthum,* while the presence of unicellular hairs on the style of *C. vietnamense* assists in separating it from *C. henryi.* The corollas of *C. scleranthum* and *C. yunnanense* are consistently glabrous, while those of *C. stellatum* are moderately to densely pubescent. It is of interest that both glabrous and pubescent corolla forms of *C. henryi* occur throughout the range of this species.

The distribution of papillae is rather uniform in the genus. They occur on the filaments of all species, and they (or at least slightly bullate cells) are frequent on the corolla, especially on the overlapping portions of the lobes. The corollas of *Craibiodendron yunnanense* are usually conspicuously papillose, thus aiding in separating this species from *C. scleranthum,* a taxon with smooth to only obscurely papillose corollas.

LEAVES

Although leaf blades tend to be quite variable in size even within a single species (e.g., 4.3–15.5 cm long in *Craibiodendron yunnanense,* 3–17 cm long in *C. stellatum*), this character is slightly useful in separating *C. scleranthum* var. *scleranthum* from var. *kwangtungense.* Lamina shape varies from ovate to obovate and typically shows much infraspecific variation. However, lamina shape is helpful in distinguishing between the varieties of *C. scleranthum* (see key), and between sterile specimens of *C. henryi* and *C. yunnanense.* The leaf apex varies from retuse or rounded to long-acuminate and is an important taxonomic character (see key); it provides a valuable means of distinguishing *C. scleranthum* from *C. yunnanense,* and *C. stellatum* from both *C. vietnamense* and *C. henryi.*

Although there are no major differences in venation pattern within the group, the secondary and tertiary veins are slightly to clearly impressed in some leaves

TABLE 3. **Character divergence values for taxa used in cladistic analyses.**

TAXON*	CHARACTER												
	A	B	C	D	E	F	G	H	I	J	K	L	Total
stellatum	1	1	1	0	0	1	1	1	0	0	1	1	8
henryi	1	1	0	0	0	1	2	1	0	0	1	1	8
vietnamense	1	1	0	0	0	1	1	1	1	1	1	1	9
yunnanense	1	0	0	0	1	0	0	0	1	0	1	1	5
scleranthum	1	0	1	0	1	0	0	0	0	0	1	1	5
kwangtungense	1	0	1	1	1	0	0	0	0	0	1	1	6

* Each taxon is indicated by its specific or varietal epithet.

but flat or slightly raised in others. This variation often provides a useful means of distinguishing between sterile specimens of *Craibiodendron henryi* and *C. yunnanense*.

Craibiodendron has lignified epidermal cells and transcurrent secondary veins (Stevens, 1971). Stevens (1969, 1971) also reported that the leaves of some plants show the development of a hypodermis and/or lignified spongy mesophyll, or fibers in the mesophyll.

INFLORESCENCES

The flowers of *Craibiodendron* are borne in distinctive axillary raceme- to paniclelike cymes on branches of the previous season. There may be one or two (rarely three) inflorescences per leaf axil. Terminal flowers are always present on the inflorescence axes, so the inflorescences are monotelic (= cymose or determinate—see Weberling, 1965). This inflorescence type is, according to Weberling (1965), more primitive than the polytelic type (= racemose or indeterminate), in which no terminal flowers are formed and the apices merely abort. Monotelic inflorescences are uncommon in the Ericaceae, occurring elsewhere only in *Elliottia* Muhlenb. ex Ell. (Bohm *et al.*, 1978) and a few species of *Agarista* (Judd, 1984). The size and structure of the cymose inflorescences of *Craibiodendron* are valuable taxonomic characters (see key). The inflorescences may be large and many-flowered with two or three branch orders (i.e., development of first- and second-order paracladia) or reduced to few-flowered racemelike structures with only one branch order (i.e., only main axis present) (see FIGURE 3). There is considerable variation in structure from the solitary lateral bibracteolate flowers (of the racemelike cymes of *C. scleranthum* var. *kwangtungense*) through short secondary branches bearing usually three to six flowers, each (except terminal flower) subtended by a small bract and with two bracteoles (in the narrow paniculate cymes of *C. yunnanense*) to elongate and branched secondary axes bearing usually seven to 30 flowers (in the broad, lax, paniclelike cymes of *C. henryi* or *C. stellatum*)—see FIGURES 3–8. The inflorescences also vary in length, from only 1–8 cm in *C. scleranthum* to 6–30 cm in *C. henryi*.

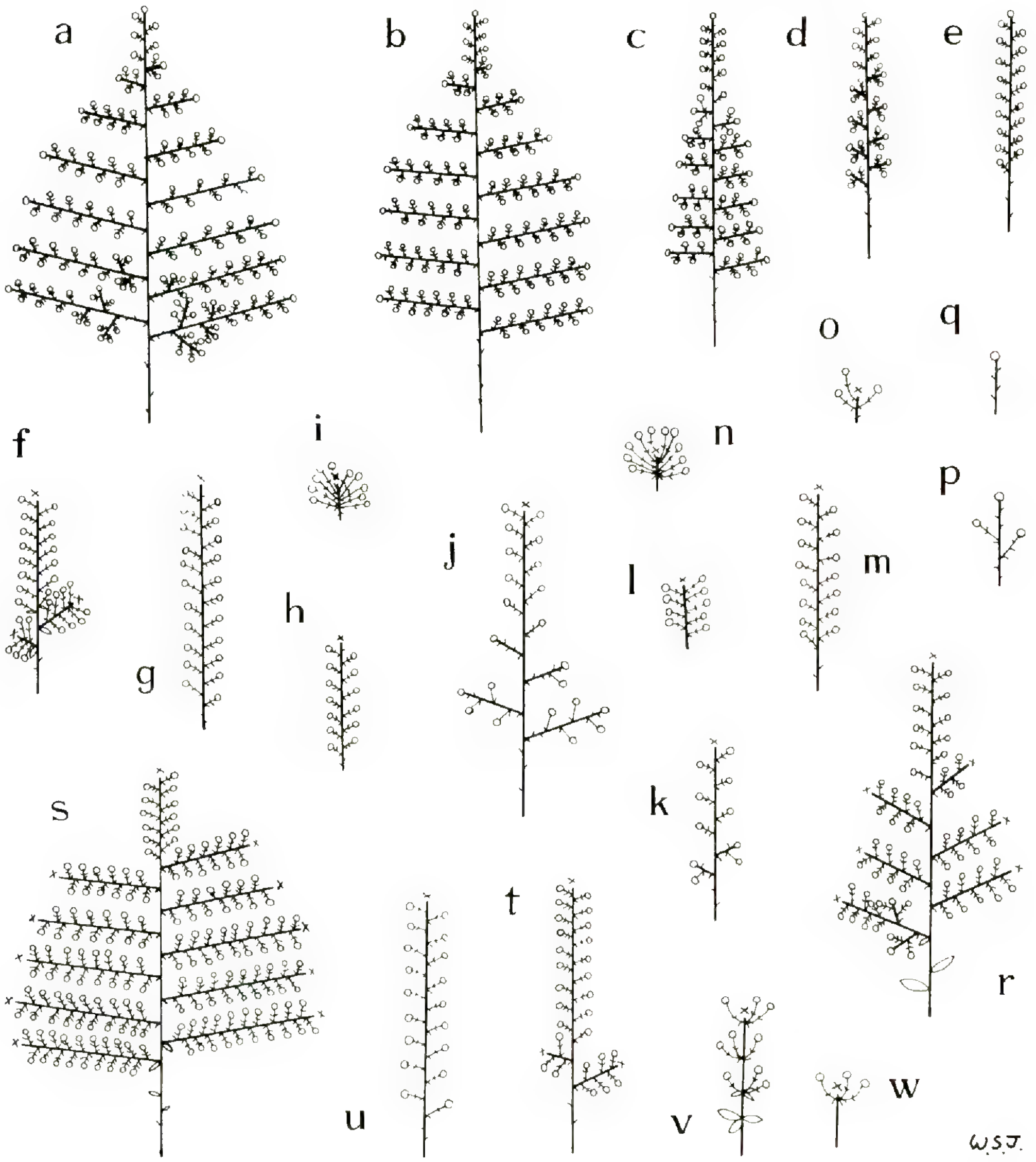


FIGURE 3. Inflorescence form in "*Lyonia* Group" of Andromedeae: a–e, *Craibiodendron,* axillary panicle- to racemelike cymes; f–i, *Lyonia,* axillary panicles, racemes, fascicles; j–r, *Agarista,* axillary or less commonly terminal panicles (sometimes partly cymose), racemes, fascicles, few-flowered clusters (with or without terminal flowers), solitary flowers; s–w, *Pieris,* axillary or terminal panicles, racemes (some with whorled flowers). Flowers indicated by circles; aborted apex (= lacking terminal flower) indicated by "x."

FLOWERS

The flowers of *Craibiodendron* are five- (rarely four- or six-)merous and usually fragrant.

The pedicel varies in length from 1 to 7 mm, showing extreme variability since it tends to elongate as the flowers and fruits develop. All species have a clearly developed articulation between the pedicel and the receptacle, its po-

sition varying from at to ca. 1.5 mm below the insertion of the calyx. The pedicel of a lateral flower is always subtended by a single bract and has two alternate to opposite bracteoles positioned from near its base to the midpoint. The number, size, shape, and position of the bracts and bracteoles associated with lateral flowers are too uniform to be useful at the species level. Flowers terminating inflorescence axes may have no bracteoles, or one or two (rarely three) of them. In other genera of Andromedeae, the distinction between bracts and bracteoles does not become arbitrary as it does in *Craibiodendron.* For example, the bracteoles of lateral flowers would be considered bracts if they each subtended higher-order flowers, as often occurs, thus forming a dichasium. Bracts and bracteoles are often quickly deciduous.

The calyx lobes show some interspecific difference in size (e.g., 1–1.3 mm wide in *Craibiodendron vietnamense,* vs. 1.2–2.3 mm in *C. henryi*), but in general there is little variation in this structure.

Corolla shape is extremely useful in delimiting infrageneric taxa within the genus (see key). The corollas of *Craibiodendron yunnanense* and *C. scleranthum* are urceolate to cylindrical with small lobes, while those of *C. stellatum, C. vietnamense,* and *C. henryi* are campanulate and more deeply lobed (especially prominently so in *C. henryi*). It varies from white (e.g., *C. stellatum* and *C. henryi*) to often red or purple (e.g., *C. yunnanense*). Its length varies from ca. 2–3.5 mm in *C. vietnamense* and *C. henryi* to 4–6 mm in *C. yunnanense.* Corolla size aids in distinguishing *C. stellatum* from *C. henryi* and *C. vietnamense,* and in differentiating these three species from *C. yunnanense* and *C. scleranthum* (see key).

Staminal-filament length ranges from 1.5–2 mm in *Craibiodendron henryi* to 3.3–4 mm in *C. yunnanense*; it is generally greater in species with urceolate flowers. Androecial characters, except for filament length, are very consistent within *Craibiodendron* and have not been used at the species level.

Ovary shape varies from ovoid to subglobose. Gynoecial characters show little variation within the genus.

Fruits and Seeds

The fruits of *Craibiodendron* are robust, thick-walled, usually five-valved, subglobose or short-ovoid, loculicidal capsules. Capsule size varies from 13–18 by 14–25 mm in *C. scleranthum* to only 6–11 by 7–13 mm in *C. yunnanense.* The distinctive seeds are large, brown, and ovoid, with a prominent unilateral wing; they have a thin testa composed of elongate cells. Seed length varies from 4–7 mm in *C. yunnanense* to 8–12.5 mm in *C. scleranthum* and is thus of some taxonomic value at the species level.

TAXONOMIC TREATMENT

Craibiodendron W. W. Smith, Rec. Bot. Surv. India **4:** 276. 1911. Type: *Craibiodendron shanicum* W. W. Smith (= *C. stellatum* (Pierre) W. W. Smith).

Nuihonia Dop *in* M. Lecomte, Fl. Gén. Indo-Chine **3:** 719. 1930. Type: *Nuihonia sclerantha* Dop (= *Craibiodendron scleranthum* (Dop) W. Judd).

Evergreen shrubs or trees with gray, shallowly and longitudinally furrowed bark. Indumentum of unicellular hairs, multicellular, biseriate-stalked hairs with small glandular heads, and papillae. Branches terete to slightly angled, often with sparse scattered gland-headed hairs, pith homogeneous. Buds often superposed, nearly hemispheric to broadly conical, with 2 (to 4) imbricate scales. Leaves alternate, simple, petiolate, convolute in bud, often reddish on young shoots; lamina coriaceous, with scattered (and often quickly deciduous) gland-headed hairs on both surfaces, often with unicellular hairs on adaxial surface of midvein, especially proximal portion, the margin entire, the venation brochidodromous, midvein impressed adaxially, secondary and tertiary veins slightly raised abaxially, tertiary veins reticulate, petiole vascular bundle bifacial. Inflorescences overwintering within bud, presumably with meiosis occurring after emergence, axillary from upper nodes of previous year's growth, of panicle- to racemelike cymes, often 2 per node; axes with scattered gland-headed hairs; flowers pendulous, perfect, 5- (rarely 4- or 6-)merous, usually fragrant, in axil of small bract or terminating axes, with 2 (on terminal flowers sometimes 0 or 1, very rarely 3) bracteoles near base to midpoint of pedicel; pedicel elongating as flower and fruit develop, with gland-headed hairs. Calyx of usually 5 imbricate lobes, articulate with pedicel, persistent in fruit, adaxially densely to moderately pubescent, abaxially with stomata, margin fringed with unicellular hairs; corolla urceolate or cylindrical to campanulate, with usually 5 short to long, imbricate lobes, carnose, cream or white to red or gray-purple, the outer surface glabrous to densely covered with unicellular hairs and with stomata, sometimes slightly papillose, the inner surface glabrous and lacking stomata; stamens usually 10, in 2 whorls, inserted at base of corolla, the filament slightly flattened, geniculate, obscurely to clearly papillose, somewhat expanded near base, lacking spurlike appendage, the anther more or less ovoid, minutely papillose to nearly smooth, lacking apical awns, dehiscing by large, introrse-terminal, elliptic pores, with white line of disintegration tissue on back of each lobe, the pollen tricolporate, in tetrahedral tetrads, without viscin strands; stigma truncate, obscurely 5-lobed, minutely papillose, the style columnar, slightly swollen near base, straight, with 5-fluted central canal, slightly impressed into apex of ovary and usually slightly exserted, the ovary superior, usually 5-locular, glabrous to densely covered with unicellular hairs, with placentae axile, subapical on persistent columella, slightly bilobed, bearing anatropous ovules; nectariferous disc an enlargement of base of ovary wall, slightly lobed. Capsules erect, thick-walled, robust, loculicidal, subglobose to short-ovoid or ovoid, sutures unthickened and not separating from valves at dehiscence, placentae persistent on columella. Seeds large, brown, ovoid with conspicuous unilateral wing, the testa thin, composed of single layer of usually elongate, thin-walled cells; embryo small, straight, more or less allantoid, white, with 2 small cotyledons, central in cross section, surrounded by fleshy endosperm.

The name *Craibiodendron* honors William G. Craib (1882–1933), of the Royal Botanic Gardens, Kew (Smith, 1911).

DISTRIBUTION. Southeast Asia—China (Tibet, Yunnan, Guangxi, Guangdong),

eastern India (Arunachal Pradesh, Meghalaya, Nagaland), and Burma, south to Laos, Thailand, Cambodia, and Vietnam.

NUMBER OF SPECIES (TAXA). 5 (6).

MEASUREMENTS AND TERMINOLOGY

All measurements (except plant height and flower color, which were taken from information given on specimen labels) included in the descriptions of species come directly from dried herbarium material. As used here, "glabrous" and "pubescent" refer to the presence or absence of unicellular hairs; the presence and distribution of multicellular, gland-headed hairs are described separately.

SPECIMENS EXAMINED

In the citation of specimens, abbreviations of institutions follow the seventh edition of *Index Herbariorum* (Holmgren, Keuken, & Schofield, 1981). In order to conserve space, only selected specimens have been cited.

KEY TO THE SPECIES OF CRAIBIODENDRON

1. Corolla 4–6 mm long, urceolate to cylindrical, glabrous, lobes less than ¼ of total length; inflorescence a raceme- to paniclelike cyme, often quite narrow, longest secondary axes with ca. 1 to 6 (to 8) flowers.
   2. Leaf apex (retuse or) rounded to acute or short-acuminate; inflorescence a racemelike cyme to a reduced paniclelike cyme, secondary axes with at most 3 flowers; capsules 13–18 by 14–25 mm; seeds 8–12.5 mm long; corolla smooth to obscurely papillose; [Guangdong and Guangxi, China; Vietnam]. . . . . 2. *C. scleranthum.*
   2. Leaf apex long-acuminate; inflorescence a paniclelike cyme, often quite narrow, longest secondary axes with usually 3 to 6 (to 8) flowers; capsules 6–11 by 7–13 mm; seeds 4–7 mm long; corolla clearly papillose; [Yunnan and Tibet, China]. . . . . 1. *C. yunnanense.*
1. Corolla 2–4.5 mm long, campanulate, glabrous to densely pubescent, lobes at least ½ of total length; inflorescence a paniclelike cyme, often quite broad, longest secondary branches with ca. 6 to 30 flowers.
   3. Leaves rounded to retuse or acute; corolla moderately to densely pubescent, 3–4.5 mm long; [southern Yunnan and Guangxi, China; Burma; Laos; Thailand; Cambodia; Vietnam]. . . . . 5. *C. stellatum.*
   3. Leaves usually long-acuminate or acuminate (rarely acute); corolla glabrous to moderately pubescent, 2–3.5 mm long.
      4. Corolla lobes more or less equal to tube, the surface clearly to obscurely papillose and sparsely to very sparsely pubescent; calyx lobes ca. 1–1.3 mm wide; style pubescent; [Vietnam]. . . . . 4. *C. vietnamense.*
      4. Corolla lobes usually much longer than tube, the surface glabrous to moderately pubescent, with papillae limited to overlapping, marginal areas of lobes; calyx lobes 1.2–2.3 mm wide; style glabrous; [India; Yunnan, China; northern Burma; northern Thailand]. . . . . 3. *C. henryi.*

1. **Craibiodendron yunnanense** W. W. Smith, Notes Roy. Bot. Gard. Edinburgh **5:** 159. 1912. TYPE: China, Yunnan, vicinity of Yunnan-sen, *E. E. Maire*

1790 (lectotype, here selected, E; photo of lectotype, B!; isolectotype, E!). FIGURE 4.

Tree or shrub to 11 m tall. Twigs glabrous to sparsely pubescent. Buds 2 per node, sometimes superposed, with 2 (to 4) scales. Leaves with petiole 2–13 mm long; blade elliptic or oblong to obovate (or ovate), 4.3–15.5 by 1.5–3.8 cm, apex long-acuminate, base cuneate and sometimes slightly attenuate, margin plane to slightly revolute near base, secondary and tertiary veins usually slightly raised to flat adaxially, midvein glabrous to sparsely pubescent near petiole (along lower ½). Inflorescences paniclelike cymes 4.5–20 cm long, with 2 orders of branches, longest secondary branches with 2 to 6 (to 8) flowers, axes essentially glabrous to sparsely pubescent. Pedicels 1–6 mm long, very sparsely to sparsely pubescent; bracteoles alternate to sometimes subopposite, near base to midpoint of pedicel, narrowly triangular to triangular-ovate, 0.5–1.9 mm long; bracts linear or narrowly triangular to narrowly ovate, 1.2–6.5 mm long, very quickly deciduous. Calyx lobes broadly ovate-triangular with acuminate to rounded-mucronate apices, 0.9–1.5 by 1.2–2.2 mm, abaxial surface glabrous; corolla urceolate to cylindrical, 4–6 by 1.5–4 mm, lobes very small in comparison with tube, cream to red or gray-purple, with abaxial surface glabrous but usually clearly papillose (especially in distal portion), thickened ridges not evident; stamens with filament 3.3–4 mm long, anther 0.7–1 mm long; ovary glabrous, style glabrous. Capsules subglobose or short-ovoid to ovoid, 6–11 by 7–13 mm, glabrous; seeds 4–7 mm long.

DISTRIBUTION AND ECOLOGY. China (Yunnan, Tibet) and northern Burma (MAP 1). Thickets and open rocky areas, temperate to warm-temperate forests, margins of coniferous forests; 1500–3200 m alt. Flowering (May) June through early August (October).

REPRESENTATIVE SPECIMENS. **Burma**: W flank of N'Maikha-Salwin divide, 26°17′N, 98°46′E, *Forrest 27053* (A, E, K), 26°15′N, 98°45′E, *Forrest 27251* (A, K, US, W). **China.** TIBET: Burma-Tibet frontier, 28°25′N, 97°55′E, *Kingdon-Ward 10149* (BM). YUNNAN: Mingkwong Valley, 25°15′N, *Forrest 7990* (BM, E, K); NW of Tengyueh, 25°10′N, *Forrest 8218* (BM, E, K, S); Shweli Valley, 25°N, *Forrest 8239* (E); Mekong and Tung-chang divide, 25°20′N, *Forrest 12131* (E); Ghi-Shan, E of Tali Lake, 25°48′N, *Forrest 13522* (BM, E, MO); Tali Range, *Forrest 15592* (A, E, K), *15626* (E, K); between Sha-yang and Chutong, 25°20′N, 99°36′E, *Forrest 21068* (A, E, K, US); Mengtze, *Henry 9182* (A, K); Lo Shiueh Mtn., Lichiang Range, *McLaren's Coll. U106* (A, BM, E, UC); Yao-chou, Tengyueh and Lungling, *Rock 7131* (A, US); between Kambaiti and Tengyueh, *Rock 7567* (A, UC, US); Shang-pa Hsien, *Tsai 54896* (A); Che-tse-lo, *Tsai 58394* (A, E); Ta-li Hsien, *Wang 71728* (A); Kuikiang Valley, Tzron, Bucahwang, *Yü 21046* (A, E).

Craibiodendron yunnanense is most closely related to the geographically isolated *C. scleranthum* (see MAP 1), from which it differs chiefly in having long-acuminate leaves, broader paniclelike cymes with longer secondary axes bearing ca. 3 to 6 (to 8) flowers, and smaller fruits and seeds. In addition, the multicellular gland-headed hairs on the abaxial leaf surface are more conspicuous in *C. yunnanense* than in *C. scleranthum*. However, sterile or fruiting specimens are often quite difficult to distinguish from the partially sympatric *C. henryi* (a species with distinctly different flowers—see key). Such material

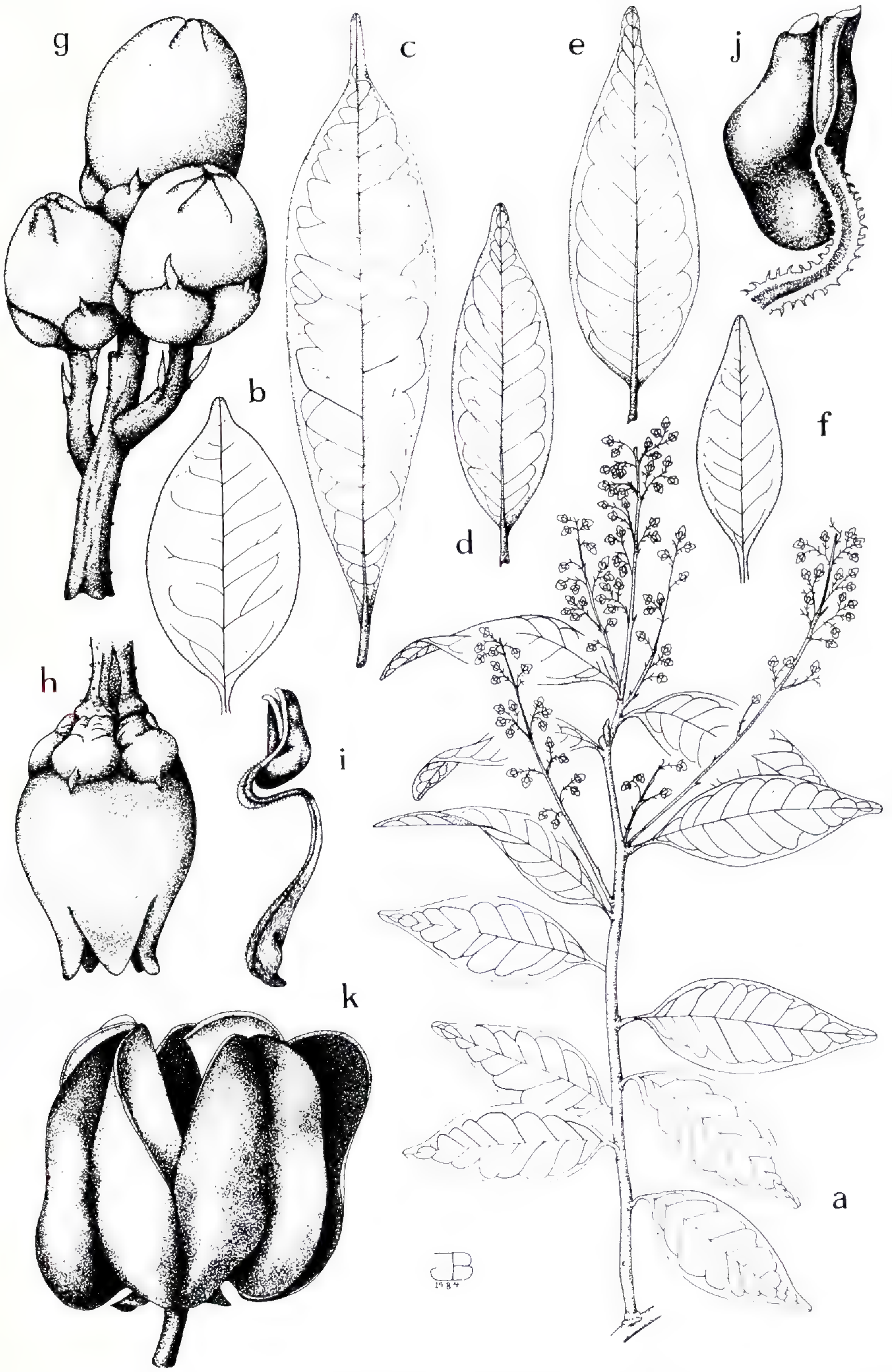
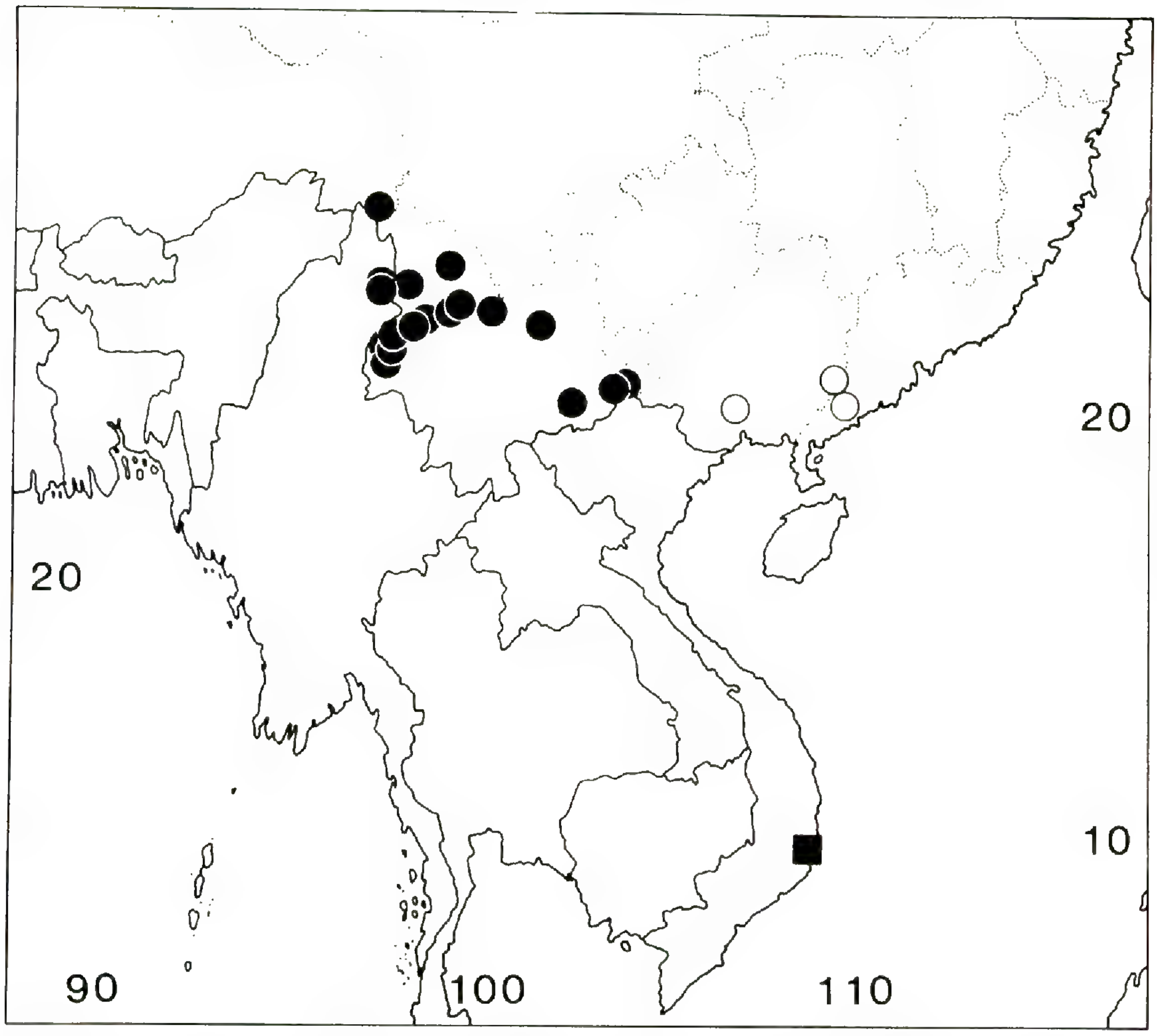


FIGURE 4. *Craibiodendron yunnanense*: a, segment of twig with inflorescences, × 0.3; b–f, leaves, × 0.5; g, dichasium, × 5; h, flower, × 5; i, stamen, × 10; j, anther, × 25; k, capsule, × 5.



MAP 1. Distribution of *Craibiodendron yunnanense* (black circles), *C. scleranthum* var. *scleranthum* (square), and *C. scleranthum* var. *kwangtungense* (open circles).

cannot be keyed, but useful characters include the more frequently elliptic to obovate leaves of *C. yunnanense* (vs. usually elliptic to ovate in *C. henryi*), the nonimpressed (vs. often impressed) secondary and tertiary veins, and the narrower infructescences.

Earlier illustrations of this species can be found in Smith (1912) and Anonymous (1974).

2. **Craibiodendron scleranthum** (Dop) W. Judd, comb. nov.

Tree or shrub to 20 m tall. Twigs glabrous to sparsely pubescent. Buds 1 or 2 per node (superposed if 2), with 2 (to 4) scales. Leaves with petiole 4–13 mm long; blade elliptic or nearly oblong to obovate or ovate, 3.2–10 by 1.2–4.6 cm, the apex (retuse or) rounded to acute or short-acuminate, the base cuneate to attenuate, the margin plane to slightly revolute, especially near base, the secondary and tertiary veins usually slightly raised adaxially, the midvein glabrous to very sparsely pubescent near petiole (along lower ½). Inflorescences racemelike or narrow (poorly branched) paniclelike cymes 1–8 cm long, with 1 or 2 orders of branches, longest secondary branches represented by single

(bracteolate) flower or with at most 3 flowers (dichasium), axes sparsely to densely pubescent. Pedicels 1–6 mm long, sparsely to densely pubescent; bracteoles alternate to opposite, at base to within lower ⅓ (occasionally to midpoint) of pedicel, narrowly triangular to linear, 0.2–1.2 mm long; bracts narrowly triangular to narrowly ovate, 0.4–2.5 mm long, deciduous. Calyx lobes broadly ovate-triangular with acuminate to acute or obtuse apices, 1.2–2(–2.5) by 1.6–2.5 mm, abaxial surface glabrous or sparsely to moderately pubescent; corolla urceolate to cylindrical, 4–6 by 2–3.5 mm, lobes small in comparison with tube, cream to red, with abaxial surface glabrous, smooth to obscurely papillose distally, thickened ridges not evident; stamens with filament 2.5–3.6 mm long, anther 0.6–1 mm long; ovary glabrous to sparsely (rarely? moderately) pubescent, style glabrous. Capsules subglobose or globose to short-ovoid, 13–18 by 14–25 mm, glabrous to very sparsely pubescent; seeds 8–12.5 mm long.

DISTRIBUTION. China (Guangdong and Guangxi) and southern Vietnam.

Key to the Varieties of *Craibiodendron scleranthum*

Abaxial surface of calyx glabrous; leaf blades 2.5–6.3 cm long, obovate to elliptic; [Vietnam]. ..... 2a. var. *scleranthum.*

Abaxial surface of calyx sparsely to densely pubescent (i.e., with unicellular hairs); leaf blades (3.6–)4–9.6 cm long, ovate to elliptic or occasionally slightly obovate; [Guangdong and Guangxi]. ..... 2b. var. *kwangtungense.*

2a. **Craibiodendron scleranthum** (Dop) W. Judd var. **scleranthum**

FIGURE 5a–c.

Nuihonia sclerantha Dop *in* M. Lecomte, Fl. Gén. Indo-Chine **3:** 719. 1930. TYPE: Vietnam, Nui-hon-heo, near Nha-trang, 3 May 1923, *E. Poilane 6236* (holotype, P; isotypes, A!, B!, K!, L(fragment)!).

Tree to 12 m tall. Leaf blades obovate to elliptic, 2.5–6.3 by 1.1–2.8 cm. Inflorescences narrow (poorly branched) panicle- to racemelike cymes, secondary branches supporting 1 to 3 flowers. Abaxial surface of calyx lobes glabrous. Capsules not seen.

See Dop (1930) for an earlier illustration of this variety.

DISTRIBUTION AND ECOLOGY. Vietnam, montane region near Nha-trang (MAP 1). Flowering in May.

REPRESENTATIVE SPECIMENS. Known only from type collection.

2b. **Craibiodendron scleranthum** (Dop) W. Judd var. **kwangtungense** (S. Y. Hu) W. Judd, comb. et stat. nov.

FIGURE 5d–l.

Craibiodendron kwangtungense S. Y. Hu, J. Arnold Arbor. **35:** 198. 1954. TYPE: China, Kwangtung [Guangdong], Ting-Wu-Shan, West River, 5 July 1928, *Y. Tsiang 792* (lectotype, here selected, A!; isolectotypes, K!, NY!, UC!, W!).

Craibiodendron kwangtungense S. Y. Hu var. *frutescens* S. Y. Hu, J. Arnold Arbor. **35:** 199. 1954. TYPE: China, Kwangsi [Guangxi], SE of Shang-sze, Shap-man-taai-shan, near Iu Shan village, 10 May 1933, *W. T. Tsang 22252* (holotype, A!; isotypes, BM!, S!).

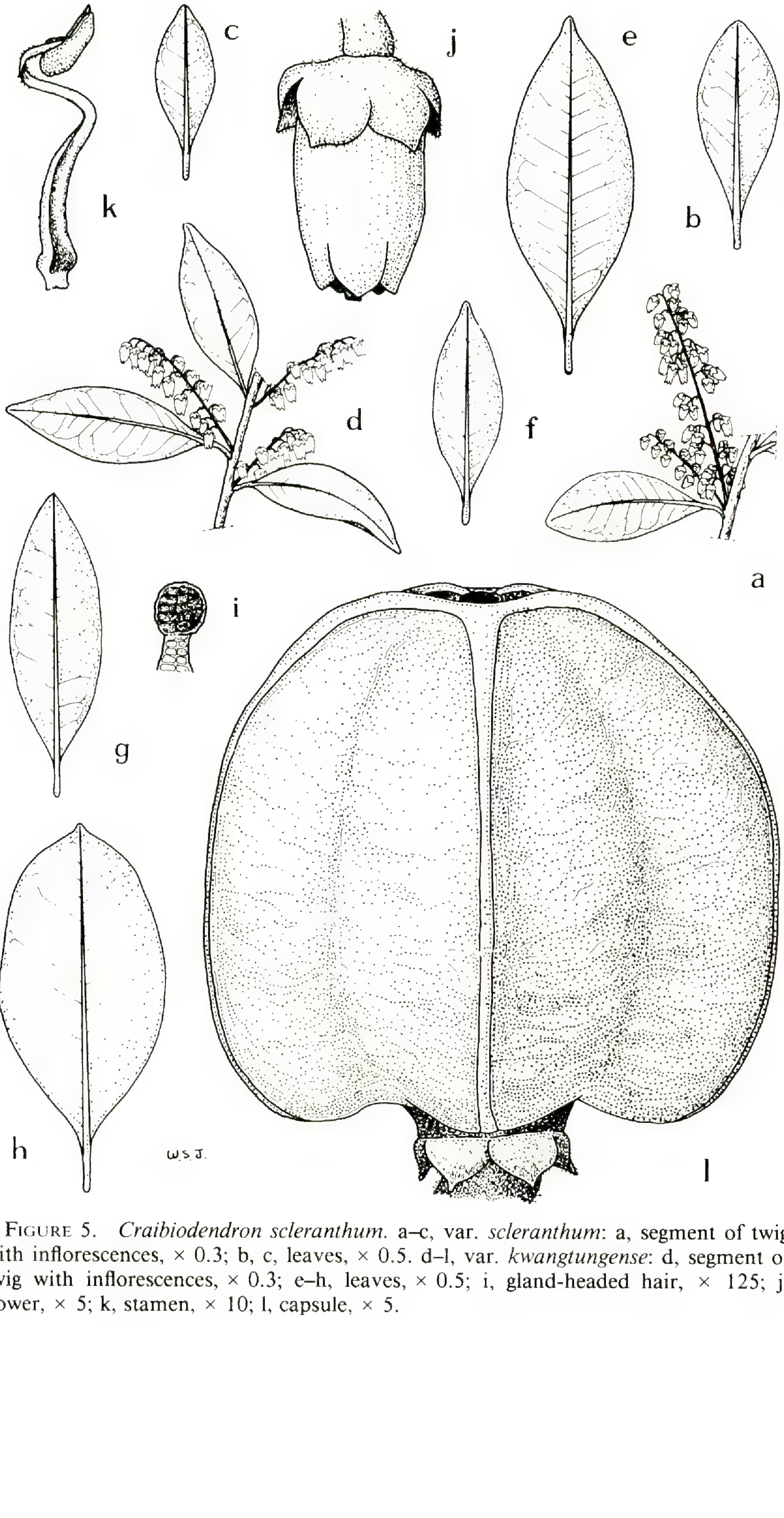


FIGURE 5. *Craibiodendron scleranthum*. a–c, var. *scleranthum*: a, segment of twig with inflorescences, × 0.3; b, c, leaves, × 0.5. d–l, var. *kwangtungense*: d, segment of twig with inflorescences, × 0.3; e–h, leaves, × 0.5; i, gland-headed hair, × 125; j, flower, × 5; k, stamen, × 10; l, capsule, × 5.

Tree or shrub to 20 m tall. Leaf blades ovate to elliptic or occasionally slightly obovate, (3.6–)4–9.6 by 1.7–4.6 cm. Inflorescences racemelike to occasionally narrow (and poorly branched) paniclelike cymes, secondary branches represented by single bracteolate flowers or 2- or 3-flowered dichasia. Abaxial surface of calyx sparsely to densely pubescent. Capsules 13–18 by 14–25 mm.

This variety was illustrated in Hu (1954).

DISTRIBUTION AND ECOLOGY. China (Guangdong and Guangxi) (MAP 1). Open shrubby areas and mixed forests, montane areas. Flowering May through June (July).

REPRESENTATIVE SPECIMENS. **China.** GUANGDONG: Ting-wu-shan, *Chun 6363* (A), *Ho 60080* (W), *Ting & Shih 635* (L), *Ying 1533* (A, UC), *1547* (A, NY, UC). GUANGXI: Seh-feng-dar Shan, S of Nan-ning, *Ching 8293* (A, E, NY, UC, US; paratype of *C. kwangtungense* S. Y. Hu).

Craibiodendron scleranthum is most closely related to *C. yunnanense* but is easily distinguished by its blunter leaf apices, fewer-flowered racemes (i.e., lateral branches only 1- to 3-flowered), less strongly papillose corollas, and larger capsules and seeds. The two species are geographically isolated (see MAP 1).

Populations of *Craibiodendron scleranthum* are separable into two morphologically distinctive and geographically separated varieties. Variety *kwangtungense* (of China) is best distinguished from var. *scleranthum* (of Vietnam) by its abaxially pubescent calyx. In the former variety the leaves are frequently slightly larger, and they are more apt to be ovate; the inflorescences are more often(?) unbranched and racemelike. Since these are the only differences between the two taxa, they are here considered to be conspecific. The correct name for the species is thus *C. scleranthum*.

3. **Craibiodendron henryi** W. W. Smith, Notes Roy. Bot. Gard. Edinburgh **5:** 158. 1912. TYPE: China, Yunnan, Szemao, 6000 ft, 6 Aug., *A. Henry 13137* (lectotype, here selected, E!; photo of lectotype, B!; isolectotypes, A!, K! (photo at NY!), NY!, US!). FIGURE 6.

Craibiodendron mannii W. W. Smith, Notes Roy. Bot. Gard. Edinburgh **5:** 159. 1912. TYPE: India, Assam [Meghalaya], Juudmaka Pahar, Jowai, near Jaintia Hills, 6000 ft, Aug. 1891, *G. Mann s.n.* (holotype, CAL, not seen; possible isotype, *King's Coll.* [*Mann*] *s.n.*, 1891, K!).

Tree or shrub to 15 m tall. Twigs glabrous to sparsely pubescent. Buds 1–3 per node (superposed if 2 or 3), with 2 (to 4) scales. Leaves with petiole 5–15 mm long; blade elliptic to oblong or ovate (to slightly obovate), 6.3–15 by 1.5–4.6 cm, the apex long-acuminate or acuminate (to acute), the base cuneate to rounded and often slightly attenuate, the margin plane to slightly revolute, especially near base, the secondary and tertiary veins slightly raised to impressed adaxially, the midvein nearly glabrous to sparsely pubescent (throughout to only near petiole). Inflorescences paniclelike cymes 6–30 cm long, with 2 or 3 orders of branches, longest secondary branches with usually (5 or) 6 to

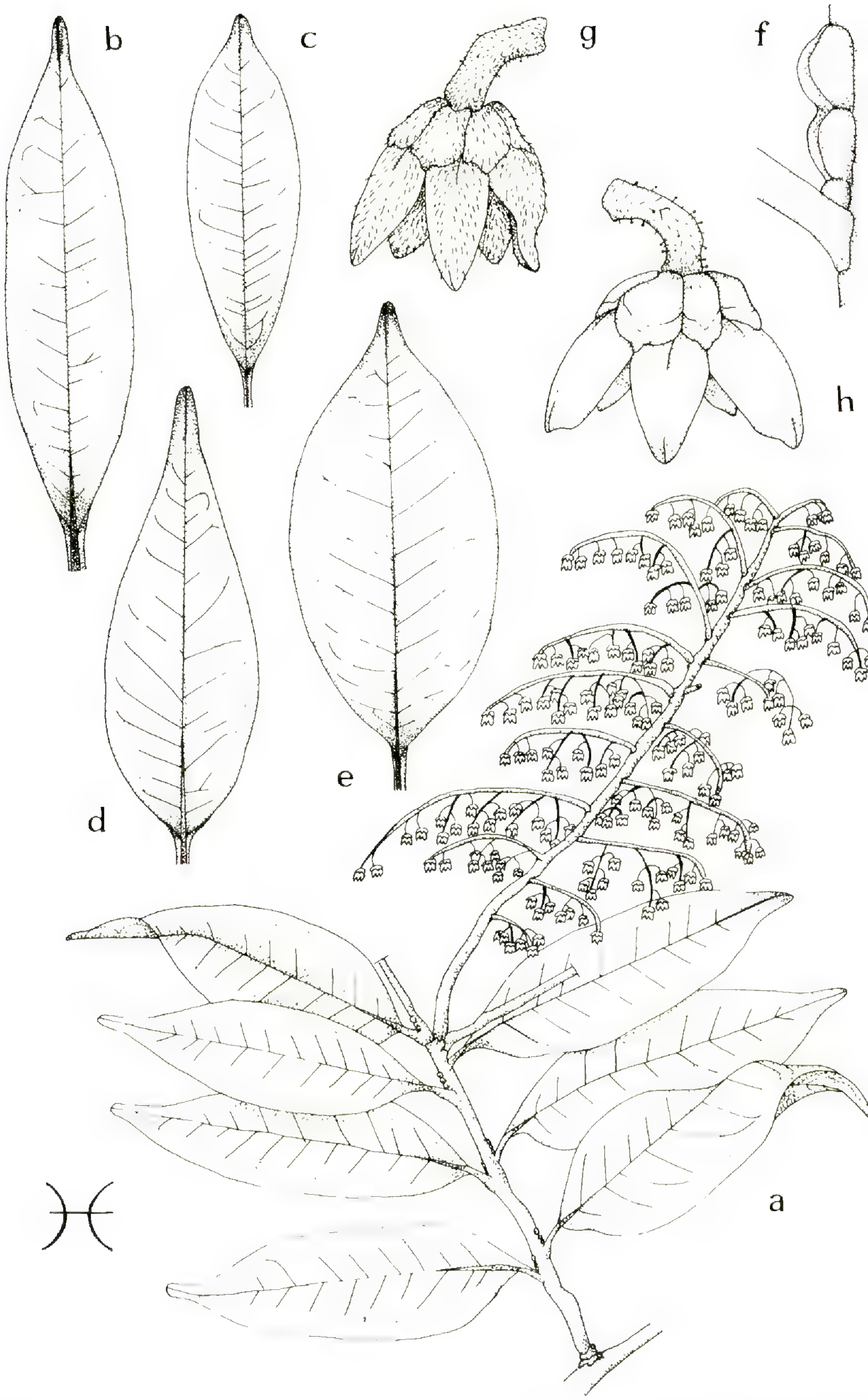
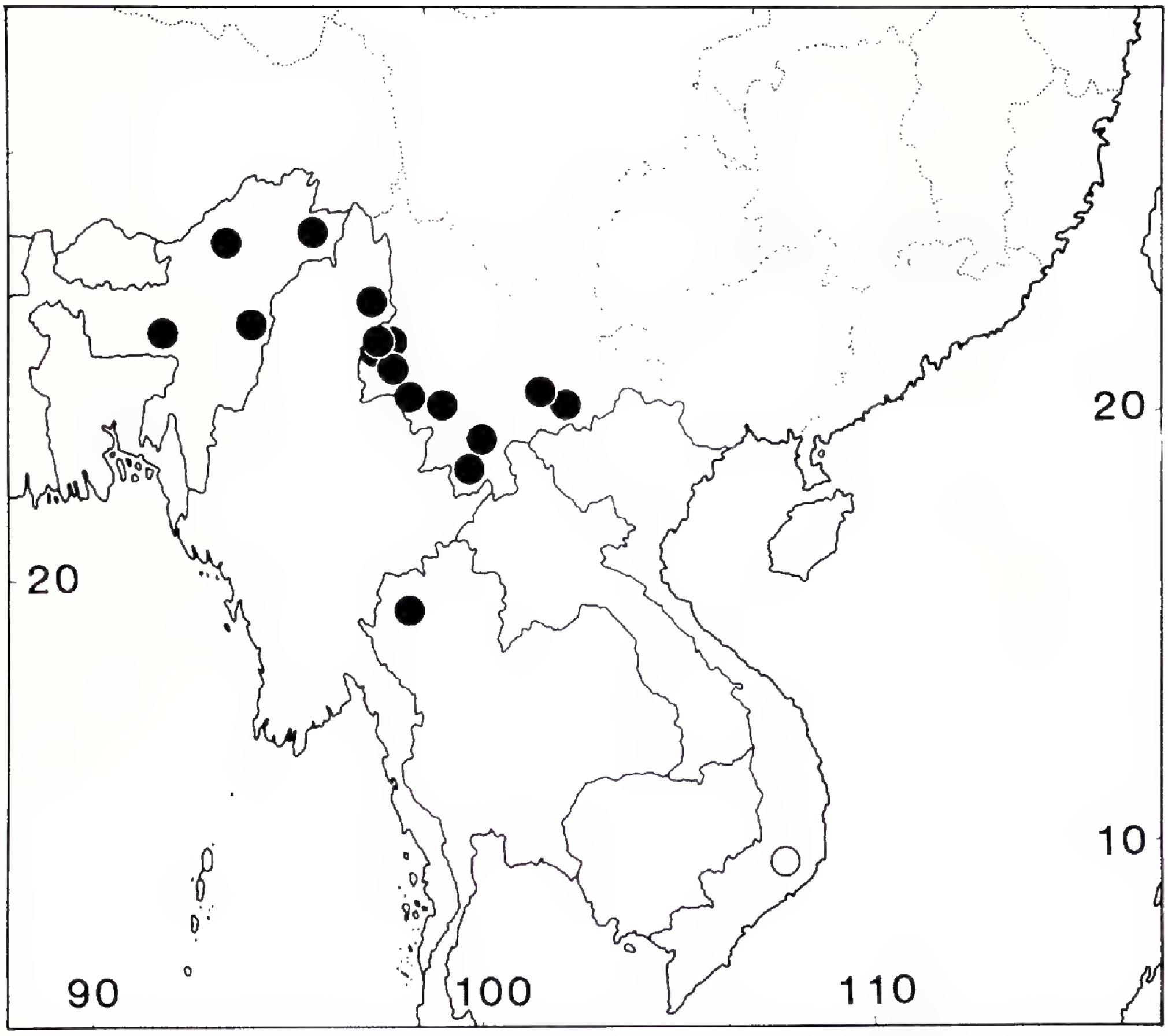


FIGURE 6. *Craibiodendron henryi*: a, segment of twig with inflorescence, × 0.3; b–e, leaves, × 0.5; f, superposed buds, × 5; g, h, flowers, × 5.



MAP 2. Distribution of *Craibiodendron henryi* (black circles) and *C. vietnamense* (open circle).

30 flowers, axes glabrous to densely pubescent. Pedicels 1–7 mm long, glabrous to densely pubescent; bracteoles alternate to subopposite, near base to midpoint of pedicel, narrowly triangular, 0.7–1.2 mm long; bracts ovate to narrowly triangular, 1.2–2.7 mm long, quickly deciduous, especially those of primary axis. Calyx lobes broadly ovate-triangular with acuminate, nearly acute, or rounded-mucronate apices, 0.8–1.5 by 1.2–2.3 mm, abaxial surface glabrous to densely pubescent; corolla campanulate, 2–3.5 by 2.1–5 mm, lobes much longer than tube, white to cream (or reddish tinged?), with abaxial surface glabrous to moderately pubescent, often obscurely papillose at margin of lobes, middle portion of each lobe sometimes with slightly thickened ridge; stamens with filament 1.5–2 mm long, anther 0.7–0.9 mm long; ovary glabrous to moderately pubescent, style glabrous. Capsules subglobose to short-ovoid, 6.5–12.5 by 9–16 mm, glabrous to sparsely pubescent; seeds 4–8.5 mm long.

DISTRIBUTION AND ECOLOGY. India (Arunachal Pradesh, Meghalaya, Nagaland), northern Burma, and northern Thailand (MAP 2). Open areas, thickets, and warm-temperate to subtropical forests; 1500–2850 m alt. Flowering (June) July through August.

REPRESENTATIVE SPECIMENS. **Burma:** Upper Burma, *Forrest 26257* (A, E, K); Htawpaw, *Sukoe 10096* (K). **China.** YUNNAN: NW of Tengyueh, 25°10′N, *Forrest 8752* (A, BM, E, K); E flank of Shweli-Salwin divide, 23°20′N, *Forrest 9434* (A, E, K); Ma-chang-kai Valley, N of Tengyueh, 25°20′N, *Forrest 9529* (A, E, K, S); Shweli-Salwin divide, 24°50′N, *Forrest 18391* (A, E, K, W); NW of Tengyueh, 25°20′N, 98°30′E, *Forrest 26136* (BM, E, K); Szemao, *Henry 9505B* (A, E, K, MO, NY); Mengtse, *Henry 10459* (A, K, paratypes of *C. henryi*); Kien-shuei Hsien, *Tsai 53196* (A); Chen-kang Hsien, *Wang 72360* (A); Fo-hai, *Wang 77404* (A); Chen-kang Snow Range, *Yü 17070* (A, E); Mienning, Po-shang, *Yü 18028* (A, E). **India.** ARUNACHAL PRADESH: W corner of Apa Tani Valley, Subansiri division, *Cox & Hutchinson 521* (K); Delei Valley, *Kingdon-Ward 7974* (K). MEGHALAYA: near Jowai, Jaintia Hills, *King's Coll.* [*Mann*] *s.n.*, 1891 (K). NAGALAND: Kekrima, Naga Hills, *Bor 2828* (K); Pedi, Naga Hills, *Bor 6271* (K). **Thailand:** Doi Angka, *Garrett 477* (A, BM, E, K, L).

Craibiodendron henryi shows greater infraspecific variability in unicellular indumentum than any other species in the genus. In some individuals the corollas are glabrous, while in others they are more or less moderately covered with unicellular hairs. The calyx and inflorescence axes also vary from glabrous to quite pubescent. Since these pubescence forms occur sporadically throughout the taxon's geographic range and are not correlated with any other morphological features, they have not been given formal taxonomic recognition. *Craibiodendron mannii,* a species described from northeastern India (see Rao & Chakraborti, 1982), is clearly conspecific, showing the distinctive combination of acuminate leaves and campanulate, deeply lobed corollas characteristic of *C. henryi.*

This species is most closely related to (and confused with) *Craibiodendron vietnamense* and *C. stellatum*; all three species have campanulate corollas with conspicuous lobes (see key). *Craibiodendron henryi* and *C. vietnamense* are allopatric, while *C. henryi* and *C. stellatum* are only marginally sympatric (see MAPS 2, 3). A few specimens from Sze-mao in Yunnan (*Henry 9505B*) show some characters of *C. stellatum* (e.g., occasional leaves with apices acute to rounded and some flowers with the lobes only slightly longer than or more or less equal to the tube). Both *C. stellatum* and *C. henryi* occur in the region of southern Yunnan, and these specimens may represent hybrids. The intermediacy of these specimens was also noted by Smith (1912).

For earlier illustrations of *Craibiodendron henryi,* see Anonymous (1974) and Rao and Chakraborti (1982, under *C. mannii*).

4. **Craibiodendron vietnamense** W. Judd, sp. nov. FIGURE 7.

Arbor ad 20 m alta. Ramuli hornotini sparsim pubescentes. Folia elliptica, oblonga vel leviter ovata, 3.4–10.2 cm longa, 1.5–4 cm lata, ad apicem acuminata, ad basin cuneata vel rotundata, ad marginem planiuscula vel leviter revoluta; petioli 7–13 mm longi. Inflorescentiae axillares, paniculatae, 7–10 cm longae, floribus terminalibus; rami secundari 7–18 floribus. Flores 5-merus. Calyx lobis 0.5–1 mm longis, 1–1.2 mm latis, abaxialiter sparsim vel moderate pubescentibus. Corolla alba, campanulata, 2.5–3.5 mm longa, 1.8–4 mm lata, lobis plus minusve aequantibus tubum, abaxialiter sparsim pubescentis, plerumque leviter papillosis. Filamenta 1.6–2 mm longa. Stylus sparsim pubescens. Capsula non visa.

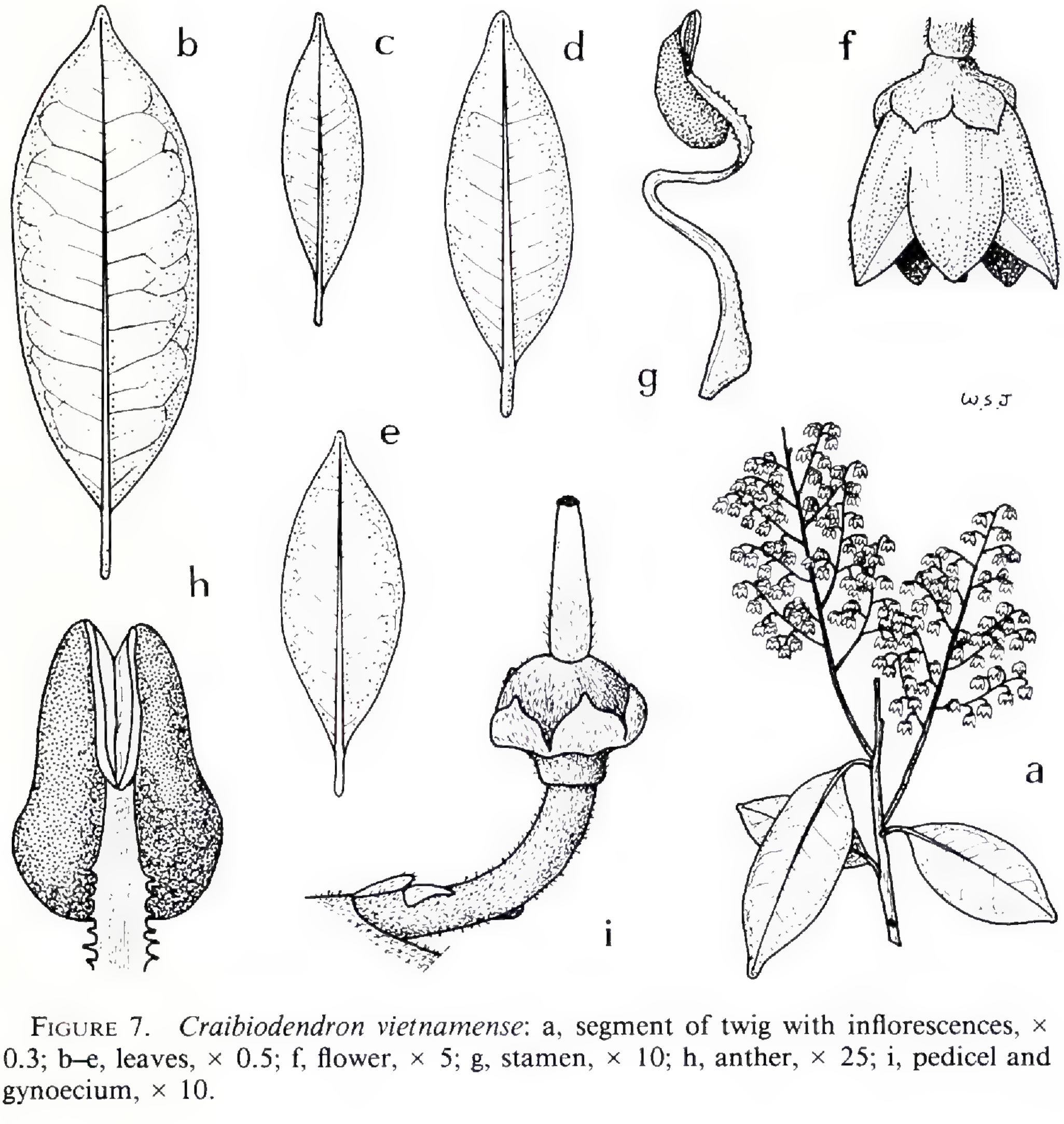


FIGURE 7. *Craibiodendron vietnamense*: a, segment of twig with inflorescences, × 0.3; b–e, leaves, × 0.5; f, flower, × 5; g, stamen, × 10; h, anther, × 25; i, pedicel and gynoecium, × 10.

Tree to 20 m tall. Twigs very sparsely to sparsely pubescent. Buds usually single, with 2 to 4 scales. Leaves with petiole 6–14 mm long; blade elliptic to oblong or slightly ovate, 3.4–10.2 by 1.5–4 cm, the apex acuminate, the base cuneate (to rounded), the margin plane to slightly revolute, especially near base, the secondary and tertiary veins slightly raised to impressed adaxially, the midvein very sparsely pubescent near petiole. Inflorescences paniclelike cymes 7–10 cm long, with 2 or 3 orders of branches, longest secondary branches with 7 to 18 flowers, axes sparsely to densely pubescent. Pedicels 1.5–4 mm long, moderately to densely pubescent; bracteoles alternate, from near base to mid-point of pedicel, broadly to narrowly triangular, 0.3–0.9 mm long; bracts triangular or narrowly so, 0.4–1.5 mm long, quickly deciduous. Calyx lobes broadly ovate-triangular with acuminate apices, 0.5–1 by 1–1.3 mm (possibly larger in fruit), abaxial surface sparsely to moderately pubescent; corolla campanulate, 2.5–3.5 by 1.8–4 mm, lobes more or less equal to tube, white, with abaxial surface very sparsely to sparsely pubescent, margin of lobes clearly papillose

to nearly smooth, middle portion of each lobe with thickened ridge; stamens with filament 1.6–2 mm long, anther 0.6–0.9 mm long; ovary moderately to densely pubescent, style sparsely pubescent. Capsules not seen.

TYPE: Annam [Vietnam], Massif du Bi-Doup, prov. Haut Donai, 2000 m, 15 Aug. 1940, *M. Poilane 30927* (holotype, L!; isotype, P).

DISTRIBUTION AND ECOLOGY. Vietnam, Bi-Doup region, 2000 m alt. (MAP 2). Probably flowering July and August.

REPRESENTATIVE SPECIMENS. **Vietnam:** Massif du Bi-Doup, *Poilane 30723* (L), *30731* (A, K, L).

Craibiodendron vietnamense is most closely related to *C. henryi* and *C. stellatum*. It is distinguished from the former by its less deeply lobed corollas and its style with a few unicellular hairs, and from the latter by its acuminate leaf apices, its slightly smaller flowers, and its pubescent style. The distinctiveness of this taxon was first recognized by Gagnepain, who considered it to be an undescribed species (unpubl. data, Herb. Leiden). The species is geographically isolated from *C. henryi* (see MAP 2); however, a southern, disjunct population of *C. stellatum* also occurs in the Bi-Doup region of Vietnam (see MAP 3).

5. **Craibiodendron stellatum** (Pierre) W. W. Smith, Kew Bull. **1914:** 129. 1914. FIGURE 8.

Schima stellata Pierre, Fl. Forest. Cochinchine **1:** *t. 122.* 1887. TYPE: Cambodia, prov. Samrong-tong, la montagne Schral, 900 m, *Pierre 853* (holotype, P; isotype, K!).

Craibiodendron shanicum W. W. Smith, Rec. Bot. Surv. India **4:** 277. 1911. TYPE: Burma, Maymyo, 3500 ft, 3 Aug. 1908, *J. H. Lace 4160* (lectotype, here selected, CAL, photo published in Smith (1912); photo of lectotype, B!; isolectotypes, E!, K!).

Tree or shrub to 12 m tall. Twigs glabrous to moderately pubescent. Buds 1 or 2 per node (superposed if 2), with 2 (to 4) scales. Leaves with petiole 3–16 mm long; blade elliptic or oblong to ovate or obovate, (3–)4–17 by (1–)1.7–8 cm, the apex retuse to rounded or acute, the base cuneate to rounded (or slightly attenuate), the margin plane to revolute, the secondary and tertiary veins slightly raised to clearly impressed adaxially, the midvein sparsely pubescent, at least proximally. Inflorescences paniclelike cymes, 5–22 cm long, with 2 or 3 orders of branches, longest secondary branches with (7 or) 8 to 25 flowers, axes moderately to densely pubescent. Pedicels 1.5–6 mm long, moderately to densely pubescent; bracteoles alternate to opposite, near base to midpoint (to near apex) of pedicel, narrowly triangular, 0.4–1 mm long; bracts ovate to narrowly elliptic, narrowly triangular, or linear, 0.8–6.5 mm long, quickly deciduous (especially those of primary axis). Calyx lobes broadly ovate-triangular with acuminate to rounded-mucronate apices, 0.8–2.5 by 1.1–2.5 mm, abaxial surface moderately to densely pubescent; corolla campanulate, 3–4.5 by 2.5–5.5 mm, lobes more or less equal to tube, white or cream, with abaxial surface moderately to densely pubescent, often obscurely papillose at margin of lobes, middle portion of each lobe usually with slightly thickened

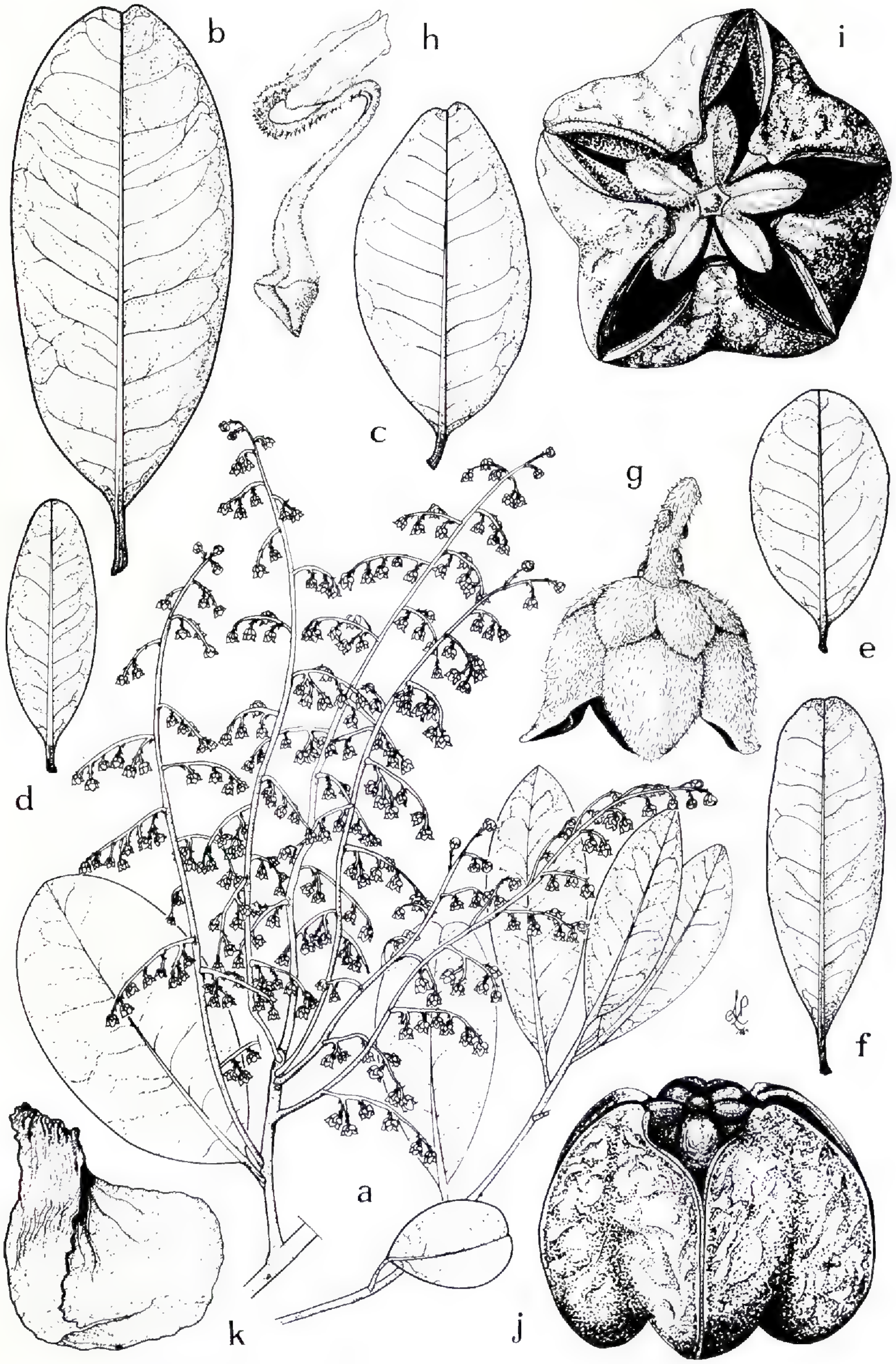
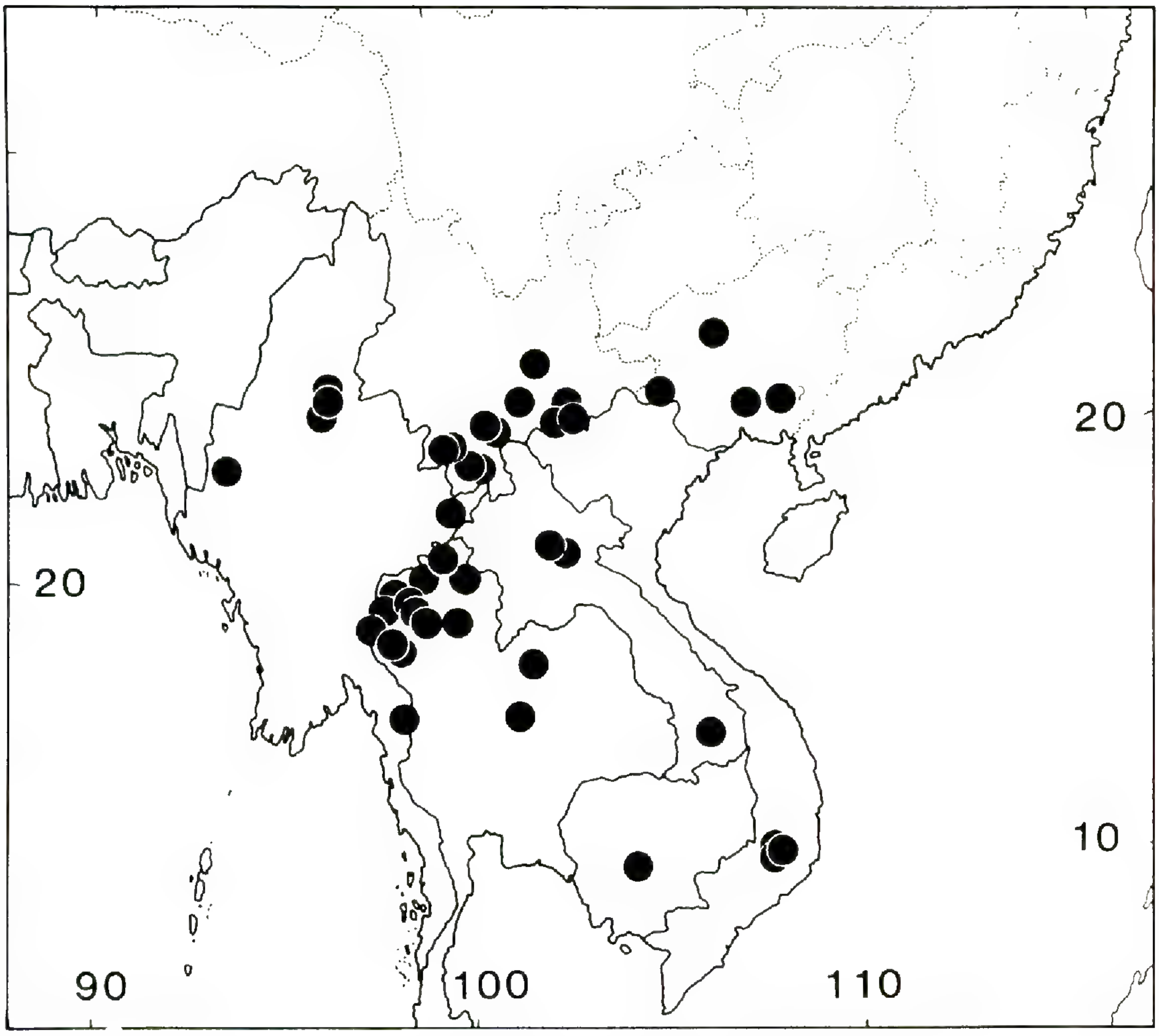


FIGURE 8. *Craibiodendron stellatum*: a, segment of twig with inflorescences, × 0.3; b–f, leaves, × 0.5; g, flower, × 5; h, stamen, × 10; i, j, capsule, top and side views, × 5; k, seed with unilateral wing, × 10.



MAP 3. Distribution of *Craibiodendron stellatum.*

ridge; stamens with filament 1.8–2.7 mm long, anther 0.7–0.9 mm long; ovary densely pubescent, style glabrous. Capsules subglobose to short-ovoid, 6–13 by 10–20 mm, very sparsely to sparsely pubescent; seeds 5–10 mm long.

DISTRIBUTION AND ECOLOGY. China (Guangxi, Yunnan), Burma, Laos, Thailand, Cambodia, and Vietnam (MAP 3). Thickets and open areas, savannas, dry dipterocarp forests, warm-temperate to subtropical forests; 200–1950 m alt. Flowering chiefly (June) July through October.

Vidal (1960) recorded that in Laos *Craibiodendron stellatum* forms a co-dominant in savannas with *Lyonia ovalifolia* (Wallich) Drude and *Castanopsis ferox* Spach and is a characteristic small tree—along with *Lyonia ovalifolia, Vaccinium exaristatum* Kurz, *Helicia balansae* Lecomte, and *Anneslea fragrans* Wallich—in forests of *Quercus* spp. and *Keteleeria roulletii* (A. Chev.) Flous. Wang (1939) reported the species as an understory shrub with species of *Lyonia, Wendlandia, Woodfordia, Eurya, Ternstroemia, Cudrania, Phyllanthus,* and *Callicarpa* in forests of *Quercus, Castanopsis, Pasania,* and *Schima.* It is also common in forests dominated by species of *Dipterocarpus.*

REPRESENTATIVE SPECIMENS. **Burma:** Falam, *Gale 9195* (E); Maymyo Hill, *Khan 117* (K); Mindat, *Kingdon-Ward 22489* (BM); Maymyo Plateau, *Lace 3128* (A, E, K); Amherst distr., Dawna Range, *Lace 5669* (E, K); Loimwe, S Shan states, *MacGregor 726* (E, paratype of *C. shanicum* W. W. Smith). **China.** GUANGXI: Chin Tung, W of Hoo-chih, *Ching 6461* (E, NY); Kwei Hoo Poo, S of Hin-yen, *Ching 7294* (E, NY); Pin-lam, *Ko 55539* (A); Chen-pien distr., *Ko 55955* (A). YUNNAN: Man-hao, *Handel-Mazzetti 5875* (W); Mengtze, *Henry 9505* (A, E, K, MO, US); E of Szemao, *Rock 2799* (A); T'sing-pien, *Tsai 52597* (A); Ping-pien Hsien, *Tsai 60560* (A, E); Che-li Hsien, *Wang 75854* (A); Lan-tsang Hsien, *Wang 76641* (A); Fo-hai, *Wang 77323* (A); Tung-hai, *Wissmann 45* (W). **Laos:** Muong-you, Luang-prabang, *Spire s.n.* (P?, reported by Vidal, 1960). **Thailand:** prov. Chiang Mai, S side of Doi Suthep, 18°50′N, 98°54′E, *Abbe et al. 9307* (A, E, L); distr. Chaiyaphum, Tunkamong, 16°20′N, 101°45′E, *Van Beusekom et al. 4361* (K, L, MO); distr. Phrae, Mae-hray, 17°45′N, 100°15′E, *Van Beusekom et al. 4819* (K, L, MO); Ban Kae, 7 km S of Mae Chem, *Hansen et al. 11052* (L); Doi Chong, 19°25′N, 98°18′E, *Hansen & Smitinand 12630* (K, L); Chiang Mai, Doi Sootep, *Kerr 1282* (BM, K, L; paratypes of *C. shanicum*), *1282A* (BM, E, K; paratypes of *C. shanicum*); Kao Krading, *Kerr 20060* (BM, E, K); S of Bo Luang, Om Koi trail, 18°04′N, 98°22′E, *Larsen et al. 1952* (L); between Hang Dong and Bo Luang, 18°17′N, 98°30′E, *Larsen et al. 2147* (L); NW of Chieng-mai, 19°N, 98°30′E, *Nooteboom 692* (K, L); Doi Chiengdao, *Put 4532* (BM, E, K, L); Pang Kia, *Rock 1604* (A, UC); Doi Sutep, Chieng-mai, *Sørensen 4805* (A, L); between Ban Khun Tan and Doi Khun Tan, *Tagawa et al. 9096* (L). **Vietnam:** Massif du Langbian, de Xomgoma à Dran, *Chevalier 38542* (L); Dalat, *Evrard 246* (A); Massif du Bi-Doup, prov. Haut-Donai, *Poilane 30248* (L); N of Dalat, prov. Haut-Donai, *Poilane 30401* (K, US).

Craibiodendron stellatum is most closely related to *C. henryi* and *C. vietnamense* and is distinguished from both by its leaves with rounded to retuse or acute (vs. usually acuminate) apices and its larger corollas. In addition, it differs from *C. henryi* in its more shallowly lobed corollas, and from *C. vietnamense* in its glabrous style. The most widely distributed species in the genus (see MAP 3), it is most common from southern Yunnan south to northern Thailand. The species is slightly sympatric (and may occasionally hybridize) with *C. henryi* at the northern edge of its range (in southern Yunnan) and occurs with *C. vietnamense* in the Bi-Doup region of Vietnam.

Craibiodendron stellatum has been more frequently collected than any of its congeners and was first to be described (see Pierre, 1887; Smith, 1911).

This species has previously been illustrated in Pierre (1887), Smith (1912), Dop (1930), and Anonymous (1974).

SPECIES EXCLUDED FROM CRAIBIODENDRON

Craibiodendron forrestii W. W. Smith, Notes Roy. Bot. Gard. Edinburgh **5**: 160. 1912. = **Quercus** sp.

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THE GENERA OF ELATINACEAE IN THE SOUTHEASTERN UNITED STATES[1]

GORDON C. TUCKER[2]

ELATINACEAE Dumortier, Anal. Fam. Pl. 44, 49. 1829, "Elatinideae," nom. cons.

(WATERWORT FAMILY)

Annual or perennial plants (up to 50 cm tall) of aquatic or moist terrestrial habitats. Roots fibrous; lower nodes usually with adventitious roots. Plants glabrous or glandular pubescent throughout, with unicellular or multicellular multiseriate capitate trichomes. Leaves opposite or decussate, entire or coarsely serrate; stomata anomocytic;[3] stipules scarious. Flowers small, actinomorphic,

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[2]Biological Survey, New York State Museum, The State Education Department, Albany, New York 12230.

[3]Tetracytic, according to Cronquist and Metcalfe & Chalk. Microscopic examination of leaves from each of the following collections revealed in all cases an anomocytic arrangement (4–8 irregularly shaped subsidiary cells around the guard cells). *Elatine Alsinastrum* L.—U.S.S.R., *Octjabreva et al. 5880* (A); *E. americana* (Pursh) Arnott—Connecticut, Bridgeport, *Eames s.n.*, 6 Aug. 1899 (GH); *E. minima* (Nutt.) Fischer & Meyer—Connecticut, Lyme, *Tucker & Linke 3176* (NYS), and Stonington, *G. C. & J. R. Tucker 3217* (NYS); *E. triandra* Schkuhr—Wyoming, Lincoln Co., *Payson & Armstrong 3434* (GH). *Bergia texana* (Hooker) Seub.—Louisiana, Red River Parish, SW of Crichton, *Thieret 20618* (LAF), and Grant Parish, SW of Montgomery, *Thieret 24749* (LAF).

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hypogynous, borne singly or in small clusters in the axils of leaves. Sepals 2–5 [or 6], free or barely united basally. Petals membranaceous, 2–5, free. Stamens [2 or] 3–6[–10], in 1 or 2 whorls, the outer whorl alternate with the petals; anthers broadly ovoid, dehiscing by longitudinal slits; pollen prolate to subspheroidal, tricolporate, 2- or 3-nucleate when shed. Ovary [2 or] 3–5-locular, ovoid to depressed ovoid; placentation axile or basal, the partitions not reaching the summit of the ovary in some species of *Bergia*; ovules numerous, anatropous, bitegmic, tenuinucellar; megagametophyte (embryo sac) of the Polygonum type. Fruit a thin-walled septifragal capsule. Seeds ellipsoid to oblong, 0.5–1.5 mm long, with finely reticulate [smooth] surfaces; endosperm very little or none; embryo straight, filling nearly the entire seed; germination epigeal. Base chromosome numbers 6, 9. TYPE GENUS: *Elatine* Linnaeus.

A small, nearly cosmopolitan family of two genera, *Bergia* L. and *Elatine,* and about 35 species. Both genera are represented in the United States. One species of *Bergia* and two of *Elatine* occur in the Southeast.

The Elatinaceae are herbaceous or suffrutescent aquatic or wetland plants with opposite [whorled] simple [tripartite or quadripartite] leaves with paired interpetiolar stipules. The inconspicuous two- to five- [or six-]merous actinomorphic flowers are borne singly or in dichasia in the upper leaf axils. The small, thin-walled capsular fruits are septifragal, and the seed coats are characteristically strongly sculptured.

Adanson noted a similarity between *Elatine* and the Caryophyllaceae in their opposite leaves, small flowers, and tiny seeds. This view was also held by De Jussieu, De Candolle, Bentham & Hooker, Bessey, and Hutchinson. As early as 1827, however, Cambessèdes noted similarities between the Elatinaceae and the Guttiferae (*sensu lato,* including the Hypericaceae). Gray, in his discussion of the taxonomy of the family, emphasized its similarities to the Guttiferae. Niedenzu, and later Melchior in succeeding editions of Engler's *Syllabus,* placed the family in the Parietales. Cronquist, Takhtajan, and Thorne concurred in the placement of the Elatinaceae in the Theales and agreed that its affinities lie with the Guttiferae (Clusiaceae). Corner noted a similarity in the structure of the seeds of the two families. The sculpturing of the seed coat in the Elatinaceae is very much like that of Guttiferae subfam. Bonnettioideae, particularly the genus *Ploiarium* Korth.

The wood anatomy of *Bergia suffruticosa* Fenzl indicates that the most likely relationship of the family is with the Guttiferae (Carlquist). The following similarities are apparent: occurrence of simple perforation plates, presence of vasicentric tracheids and fibriform vessel elements, predominance of uniseriate rays, vertical orientation of scalariform vessel–ray pitting, absence of intraxylary phloem, presence of brownish compounds [tannins?] in the parenchyma, and occurrence of druses and solitary crystals.

Melikian & Dildarian, on the basis of anatomical and palynological studies, and Walia & Kapil, on the basis of embryological studies of the Frankeniaceae, a family usually placed in the Parietales, concluded that the Elatinaceae and the Frankeniaceae are closely related. However, because several of the similarities they listed (e.g., trinucleate pollen, bitegmic ovules, and monosporic

embryo sacs) characterize many families of angiosperms, a close relationship between the Frankeniaceae and Elatinaceae seems doubtful.

The family is little known chemically (Gibbs, Hegnauer). Several phenolic acids (delphinidin, ellagic acid, quercetin, cyanidin, kaempferol) have been reported from *Bergia* (species not indicated); saponins and alkaloids are absent from *Bergia,* while tannins occur in at least two species. *Bergia suffruticosa* has been found to lack alkaloids. *Elatine* appears to be poor in taxonomically interesting chemicals: *E. gratioloides* A. Cunn. contains no alkaloids, saponins, or leucoanthocyanins; *E. hexandra* (Lapierre) DC. contains ellagic acid but lacks other phenolic compounds. The petals of *E. americana* (Fernald) and *E. minima* (pers. obs.) are sometimes pinkish, probably because of anthocyanins. Gibbs reported druses and raphides to be absent in the family, while Metcalfe & Chalk noted the occurrence of cluster crystals in the endodermis and pith of *Bergia* (species not indicated), and Carlquist recorded druses and solitary crystals in the parenchyma of *B. suffruticosa.*

The family is of little economic importance. No species is recorded as being gathered for use as food or condiments, nor is any reported to be poisonous to humans or livestock. *Bergia suffruticosa,* $2n = 36$, is employed in Pakistan in folk medicine and in Sudan as a poultice for broken bones.

Several species of *Bergia* are weeds in rice fields in the Old World, as are species of *Elatine* in California, Japan, and Java. The seeds and foliage of *Elatine* are eaten by ducks, and the plants are considered to be beneficial because they consolidate mud and provide cover for small fish. Several species (e.g., *E. Hydropiper* L. and *E. triandra*) are cultivated as "turf-forming" foliage plants in aquaria. They are reported to be easy to propagate from either cuttings or seed.

The family is poorly known taxonomically. A comprehensive worldwide revisionary study of *Bergia* has never been made. The only global monograph of *Elatine* appeared in the 1870's (Dumortier). Niedenzu's account of the Elatinaceae in *Die Natürlichen Pflanzenfamilien* is of limited use for the identification of specimens because of its synoptic nature. Most taxonomic investigation in this family has either involved floristics or been concerned chiefly with the description of new taxa. Most workers seem to have been familiar only with the species represented in their herbaria.

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KEY TO THE GENERA OF ELATINACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *small, soft, herbaceous or woody-based annual or subperennial plants growing in or near water; glabrous or glandular pubescent throughout; leaves*

opposite, decussate, stipules scarious; flowers inconspicuous, borne singly or in small axillary clusters; sepals and petals 3–5; ovaries globose to ovoid; styles very short; capsules septifragal; seeds small, more or less reticulate.

Plants glandular pubescent throughout; flowers 5-merous; sepals acute, with a conspicuous, thickened midrib; capsules ovoid. ..... 1. *Bergia.*

Plants glabrous; flowers 2–4-merous; sepals obtuse, without a visible midrib; capsules globose or depressed globose. ..... 2. *Elatine.*

1. **Bergia** Linnaeus, Mant. Pl. **2:** 152. 1771.

Annual [or perennial], herbaceous [or suffrutescent], simple to much-branched procumbent to ascendent plants of moist, disturbed soils; often occurring on sand bars along rivers. Roots fibrous, much branched from a conspicuous taproot; adventitious roots usually formed in the axils of the lower leaves. Stems herbaceous but woody and thickened at base, glandular pubescent throughout. Leaves decussate, glandular pubescent on both surfaces [or glabrous], the margins serrate; stipules scarious, glandular pubescent. Flowers solitary or in dichasia in the axils of the leaves. Sepals 5, free, acute, mucronate, with a thickened midvein and scarious margins, glandular pubescent throughout. Petals 5, oblong, membranaceous, glabrous, whitish. Stamens 5 [or 10]; anthers ellipsoid; pollen tricolpate, subprolate to spheroidal, sexine reticulate to reticulate-polybrochate, binucleate when shed. Ovary ovoid, 5 [or 6]-locular [the partitions not reaching the summit in some Asian species], each locule with numerous ovules; stigmas 5; styles 5, very short. Seeds oblong, slightly curved, brown, obscurely reticulate [smooth]. Base chromosome number 6. TYPE SPECIES: *B. capensis* L. (Named for Peter Jonas Bergius, 1730–1790, Swedish botanist and student of Linnaeus.)

A genus of about 25 species, primarily of the Old World tropics. Three species occur in the New World: *Bergia arenarioides* Camb. in Brazil; *B. capensis,* $2n = 18$, native to Africa and southern Asia, collected as an adventive on the Pacific coast of South America (Molau); and *B. texana* (Hooker) Seub., ranging from Illinois, Missouri, Arkansas (Desha County), and Louisiana (Bossier, Red River, St. Mary, and Grant parishes), westward to northern Mexico, southern California, and eastern Washington.

The center of greatest diversity in the genus is in eastern and southern Africa, where some 20 species occur. By contrast, there are only five species in southern Asia and two in Malesia and Australia. *Bergia capensis,* which ranges from southern Africa to India and Indonesia, is the most widely distributed species in the genus. It is also recorded as an adventive weed in rice fields in Spain and Portugal.

Niedenzu divided the genus into two sections. He placed *Bergia texana* in sect. BERGIA (sect. *Dichasianthae* Niedz.), in which the flowers are borne in axillary dichasia. Species of sect. MONANTHAE Niedz. are characterized by solitary axillary flowers.

Apparently nothing is known about the pollination biology of any species of *Bergia.*

About half the species of *Bergia* are aquatic; the remainder are plants of

moist soils. According to D'Almeida, *B. capensis* has dimorphic roots. The plumose water roots lack root hairs but frequently have chloroplasts in the cortex and thus supplement the leaves as assimilatory organs. The stout whitish roots that anchor the plant in the muddy bottom of the pond or pool bear very few lateral roots but are almost completely covered by root hairs.

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2. **Elatine** Linnaeus, Sp. Pl. **1:** 367. 1753; Gen. Pl. ed. 5. 172. 1754.

Small, aquatic or emergent, herbaceous annuals or short-lived perennials of marshes, streambanks, shores of lakes and ponds, mud flats, pools, ditches, and rice fields. Roots slender, soft, the exposed portions sometimes with chloroplasts in the cortical cells. Stems soft, chlorophyllous, with 5–11 air chambers visible in cross section; stems upright when growing underwater, more or less procumbent when growing on wet soil or mud. Leaves opposite, sessile or with short petioles, blades narrowly to broadly elliptic to nearly orbiculate, one-fourth to three-fourths as long as wide, entire or essentially so (with hydathodes on the margins at the ends of the veins), the apices rounded, the bases cuneate to somewhat rounded. Flowers solitary in the axils of the upper leaves, [2 or]

3 [or 4]-merous. Sepals membranaceous, very pale green, inconspicuous. Petals the same number as sepals, membranaceous, pale greenish white, about as long as the sepals [small floral nectaries present in some species]. Stamens [2 or] 3[–8]; filaments about half as long as to equaling the petals; anthers tetrasporangiate (sometimes bi- or trisporangiate in cleistogamous flowers), broadly ovoid, the connective apex subacute, prolonged slightly beyond the anther locules; pollen tricolporate, spheroidal to subprolate, sexine granulate to reticulate, trinucleate when shed. Ovaries broadly ovoid, [2 or] 3 [or 4]-locular, the partitions thin, fragile; placentation basal [axile]; styles 3; stigmas terminal, appressed to the ovary. Capsules subglobose or depressed ovoid, the walls thin, membranaceous, delicate, the seeds more or less visible within. Seeds cylindrical, straight or slightly curved, narrowly to broadly ellipsoid, the surface brown to yellowish brown, reticulate with a network of fine ridges forming hexagons [ovals]. Base chromosome number 9. LECTOTYPE SPECIES: *E. Hydropiper* L.; see Britton & Brown, Illus. Fl. No. U. S. & Canada. ed. 2. **2:** 538. 1913; also see Hitchcock & Green. (*Elatine,* a Greek plant name employed by Dioscorides and Tournefort and adopted by Linnaeus [Crit. Bot. 103. 1737; Philos. Bot. 144, 174. 1751]; also see Dumortier, Gray.)—WATERWORT, PIGMY MUDWORT.

A genus of about 25 species, interruptedly cosmopolitan in distribution, with species occurring on all continents except Antarctica. Ten species are native to North America and about 12 to Eurasia. There are five to seven species in South America, mostly in temperate and Andean regions. Three primarily European species occur in North Africa; none apparently grows in the central part of the continent, while two are reported from Zimbabwe and Namibia (Riley). Two species occur in India and Malesia; one, *Elatine gratioloides* Bentham, is found in Australia, New Zealand, and Fiji.

Two subgenera and three sections were named by Seubert, whose classification was followed by Niedenzu in *Die Natürlichen Pflanzenfamilien.* Subgenus POTAMOPITYS (Adanson) Seub., containing only *Elatine Alsinastrum* of Europe and North Africa, is characterized by having whorled leaves. The remaining species, all of which have opposite leaves, comprise subg. ELATINE (subg. *Hydropiper* Moesz). Subgenus ELATINE contains two sections. Section ELATINE (sect. *Elatinella* Seub.), in which the flowers have six to eight stamens in two whorls, includes about eight species of Eurasia, California (*E. heterandra*), and South America (*E. ecuadoriensis*). The remaining species, which have two or three stamens in one whorl, comprise sect. CRYPTA (Nutt.) Seub. and occupy nearly the total range of the genus. All North American species (except *E. heterandra,* q.v.) are included in this section. *Elatine heterandra* may have either three or six stamens per flower (Mason), thus shedding doubt on the reliability of stamen number in classification.

Two species occur in the Southeast.[4] *Elatine americana* is known from col-

[4]The taxonomy used here follows Fernald (1917, 1941). An examination of numerous herbarium specimens (at A, CCNL, GA, GH, LAF, NEBC, and NYS) shows that *Elatine brachysperma* and *E. americana* are distinguishable on the basis of seed shape and pitting. Fassett (and Gleason) treated these species as varieties of the primarily Eurasian *E. triandra.*

lections in Jackson Co., North Carolina, and Vermillion Parish, Louisiana. It ranges northward to Newfoundland and southeastern Manitoba. It is also common in Australia and New Zealand (Moore & Betche, Cheeseman, Good). More recently, Aston treated these Southern Hemisphere populations as a species, *E. gratioloides,* but her description and illustration seem indistinguishable from those of *E. americana.*

The other southeastern species, *Elatine brachysperma,* occurs from Georgia westward to California. Specimens have been seen from Georgia (Hancock and Oglethorpe counties), Alabama (Perry County), and Louisiana (Cameron and Lafayette parishes).

Two additional species occur in northeastern North America. *Elatine minima* has a wide range, from Labrador to the Northwest Territories, southward to Virginia and Illinois. *Elatine triandra,* a Eurasian and western North American species, has been collected in Skowhegan, Maine, and Brooklyn, New York; in both localities it is believed to be an introduction from Europe. Five species—two endemic to California—occur in western North America.

Plants of *Elatine* grow as submersed or emergent plants in shallow fresh [brackish or alkaline] pools, lakes, ponds, and ditches. They often occur in artificial ponds that are seasonally drained or in natural pools that dry out. Many species show some adaptation to fluctuating water levels in having plants with different growth forms under water and on land. The most striking example of this dimorphism occurs in the European *E. Alsinastrum,* the only species with whorled leaves. The upper, emergent portion of the stem bears whorls of leaves with ovate blades 1–2 cm long, while the submersed lower stem has leaves divided into four capillary segments, thus giving the appearance of 12 leaves per node. In the remaining species terrestrial and aquatic forms are less different. In *E. americana* and *E. brachysperma* submersed plants have longer internodes and longer, narrower leaf blades and are darker green than littoral plants (Bicknell, Sculthorpe; illustrations in Fassett and Kupper & Gams).

Knowledge of the pollination biology of *Elatine* is incomplete. Cleistogamous underwater flowers are present in many species (Duncan recorded them in populations of *E. americana* in Georgia). Chasmogamous flowers have small nectaries, but no report of insect visitors has been found. Self-pollination in *E. hexandra,* $2n = 72$, is effected as the filaments elongate, bringing the anthers into contact with the stigmas (Hutchinson, 1955; Knuth). Self-pollination has been observed to occur in the same manner in plants of *E. minima* collected and grown indoors at the New York State Museum (collection from Stonington, Connecticut, *G. C. & J. R. Tucker 3217* [NYS]). In the cleistogamous flowers of *E. triandra,* $2n = 40$, and *E. hexandra* the anthers are brought into contact with the stigmas as the filaments elongate. The pollen grains germinate *in situ,* and the tubes grow through the anther wall into the stigma (Frisendahl).

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NEW SPECIES OF CERATOSTEMA (ERICACEAE: VACCINIEAE) FROM THE NORTHERN ANDES

JAMES L. LUTEYN[1]

Ceratostema is a genus of primarily Andean blueberries consisting of 23 species. Most are found in eastern Ecuador, but one is endemic to southern Colombia, two to northern Peru, and one to the Guayana Highland in western Guyana. The plants are scandent or, more commonly, erect shrubs to 3.5 m tall. They may be terrestrial or sometimes epiphytic and possess large (2–5 cm long), fleshy, waxy corollas in striking shades of bright red or orange. Some have colorful floral bracts; others, large superficial or subsurface woody burls. All are probably hummingbird pollinated. The genus is of little economic importance. *Ceratostema alatum,* commonly known as "pera silvestre" or "manzanilla" in Tungurahua Province, Ecuador, is eaten locally; the flavor suggests that of the pear (Popenoe, 1924). I have collected fruits of *C. alberti-smithii* that measured about 3–3.5 cm in diameter and were very juicy although not particularly sweet.

The genus was first described by A.-L. de Jussieu in 1789, the name referring to the long "horned stamen" (the "horns" are the long anther tubules). It was last treated by A. C. Smith (1952), who gave a brief discussion and a key to the 16 species then recognized. It is characterized by: calyx articulate with the pedicel (articulation obscure in one species); corolla large and usually conspicuously ventricose basally, deeply lobed, the lobes usually very long and narrow; stamens with the filaments distinct or connate, the thecae strongly granular (or papillate), and the tubules very long and thin, dehiscent by short, oblique clefts. *Ceratostema* is most closely related to *Semiramisia* Klotzsch, as was discussed by Luteyn (1984).

KEY TO THE SPECIES OF CERATOSTEMA

1. Leaves basally attenuate, acute, or rounded, not cordate and amplexicaul.
   2. Calyx limb very conspicuous, lobes at least 10 mm long.
      3. Hypanthium terete, not costate or winged.
         4. Flowers 4-merous; leaf blade 4–6 × 1.2–1.8 cm; flowers solitary or paired, corolla lobes ca. 20 mm long. ..... *C. flexuosum* (A. C. Smith) Macbr.
         4. Flowers 5-merous; leaf blade 9–13 × 3–5 cm; flowers in fascicles of 4 to 6, corolla lobes 4–7 mm long. ..... *C. fasciculatum* Luteyn.
      3. Hypanthium 10-costate or winged.

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5. Hypanthium 10-costate. ..... *C. alberti-smithii* (Sleumer) Sleumer.
5. Hypanthium clearly winged.
6. Leaves glabrous beneath; calyx 30–45 mm long; flowers racemose, essentially glabrous. ..... *C. reginaldii* (Sleumer) A. C. Smith.
6. Leaves soft-pilose beneath; calyx ca. 18 mm long; flowers solitary, densely pilose. ..... *C. lanceolatum* Bentham.

2. Calyx limb comparatively inconspicuous, lobes 1–7 mm long.
7. Calyx lobes minute, scarcely 1 mm long, sinuses flattened.
8. Hypanthium 5-winged; corolla 30 mm long, lobes 7–8 mm broad at base; leaves pinnately nerved. ..... *C. charianthum* A. C. Smith.
8. Hypanthium not winged; corolla 45–55 mm long, lobes 3 mm broad at base; leaves plinerved. ..... *C. prietoi* A. C. Smith.
7. Calyx lobes obvious, 1–7 mm long, sinuses acute or obtuse.
9. Corolla 15–20 mm long; calyx continuous with pedicel. ..... *C. loranthiflorum* Bentham.
9. Corolla 33 mm or more long; calyx articulate with pedicel.
10. Calyx and corolla covered by gland-tipped hairs; Venezuela. ..... *C. glanduliferum* Maguire, Steyerm., & Luteyn.
10. Calyx and corolla without gland-tipped hairs; Ecuador and Peru.
11. Leaves 6–12 cm long, plinerved.
12. Hypanthium conspicuously 10-costate; calyx lobes ca. 6 mm long; corolla weakly ventricose, ca. 6 mm in diameter near base; filaments ca. 3 mm long. ..... *C. calycinum* (A. C. Smith) Sleumer.
12. Hypanthium terete or only inconspicuously 5-angled; calyx lobes 2–3.5 mm long; corolla strongly ventricose, 8–17 mm in diameter near base; filaments ca. 5 mm long. ..... *C. ventricosum* A. C. Smith.
11. Leaves 2–6 cm long, pinnately nerved.
13. Leaves revolute and usually serrate or crenulate; hypanthium narrowly winged; calyx lobes ca. 2 mm or less long. ..... *C. alatum* (Hoer.) Sleumer.
13. Leaves flat and entire; hypanthium terete or only angled, not winged; calyx lobes 5–7 mm long.
14. Hypanthium and corolla terete; calyx lobes marginally glandular; corolla essentially glabrous; filaments connate. ..... *C. nubigenum* A. C. Smith.
14. Hypanthium and corolla 5-angled; calyx lobes eglandular; corolla villose; filaments distinct. ..... *C. campii* A. C. Smith.

1. Leaves cordate and usually amplexicaul.
15. Calyx limb very conspicuous, lobes at least 10 mm long.
16. Hypanthium terete.
17. Leaves usually densely soft-pilose beneath; bracteoles median, 5–8 mm long; calyx lobes 10–17 mm long; filaments distinct. ..... *C. callistum* A. C. Smith.
17. Leaves essentially glabrous beneath; bracteoles apical, up to 17 mm long; calyx lobes 10 mm long; filaments connate. ..... *C. pensile* (A. C. Smith) A. C. Smith.
16. Hypanthium 10-costate.
18. Floral bracts 4.5–7 cm long, persistent and covering flowers at anthesis; bracteoles 3.5–4.5 × 1 cm; pedicels 10–12 mm long. ..... *C. megabracteatum* Luteyn.

18. Floral bracts 2–2.5 cm long, caducous; bracteoles 1.5–2.5 × 0.3–0.5 cm; pedicels 30–40 mm long. ..... *C. peruvianum* Gmelin.

15. Calyx limb comparatively inconspicuous, lobes 1–7 mm long.
19. Floral bracts 40–50 mm long, persistent and covering flowers at anthesis. ..... *C. nodosum* Luteyn.
19. Floral bracts 2–8 mm long, usually caducous and much shorter than flowers at anthesis.
20. Leaves shallowly cordate, only slightly amplexicaul; inflorescences fasciculate. ..... *C. lanigerum* (Sleumer) Luteyn.
20. Leaves deeply cordate, strongly amplexicaul; inflorescences racemose.
21. Leaves bullate, apically long-acuminate, basally auriculate with the lobes well separated, not imbricate. ..... *C. ferreyrae* Luteyn.
21. Leaves flat, apically obtuse or acute, basally auriculate-clasping with the lobes conspicuously imbricate.
22. Branches and leaves glabrous beneath; leaves 9–13.5 × 5–7 cm; hypanthium ± terete, inconspicuously costate; calyx lobes wide spreading, usually reflexed at anthesis. ..... *C. silvicola* A. C. Smith.
22. Branches and leaves shortly white-pilose beneath; leaves 5–7.5 × 3–4.5 cm; hypanthium conspicuously 10-costate; calyx lobes spreading or erect but not reflexed at anthesis. ..... *C. amplexicaule* A. C. Smith.

NEW TAXA

Ceratostema ferreyrae Luteyn, sp. nov. FIGURE 1.

A C. lanigero foliis profunde cordatis amplexicaulibus longe acuminatis bullatis nec cordatis vix amplexicaulibus breviter acuminatis, inflorescentiis racemosis nec fasciculatis, et distributione geographica differt.

Shrub; stems subterete, smooth, nitid, grayish- to reddish-brown when dry, glabrous; twigs subterete, complanate, minutely striate, densely pilose-hirsute with unicellular white hairs to 1.2 mm long. Leaves with petiole 3–5 mm long, subterete, flattened abaxially, rugose, hirsute; blade narrowly ovate to lanceolate, 12–20 × 3–5.5 cm, coriaceous, bullate, the apex long-acuminate, the base broadly and deeply cordate, auriculate with lobes well separated, amplexicaul, the margin entire, the surfaces weakly hirsute along veins, the venation pinnate, with 1 or 2 lateral veins per side but these anastomosing near base to form reticulate pattern throughout, midrib and lateral veins usually conspicuously impressed above and raised beneath, veinlets slightly raised on both surfaces. Inflorescence solitary, axillary, racemose, all portions hirsute with unicellular white hairs, 3- or 4-flowered, flowers clustered distally; rachis 2–2.5 cm long, terete, striate; floral bracts narrowly lanceolate, long-acuminate, 4–5 mm long; pedicels 3.5–4.5 cm long, subterete, striate; bracteoles basal, 1.5–3 mm long, aristate. Calyx conspicuously articulate with pedicel, 6.5–7 mm long, the hypanthium subcylindrical, ca. 4 mm long, 10-costate, the limb campanulate, ca. 2.5–3 mm long including lobes, the lobes triangular, acute, ca. 2 mm long, the sinuses acute; corolla subcylindrical, basally swollen, 43–45 mm long, the tube red when fresh, the lobes narrowly triangular, long-acuminate, 15–17 mm long,

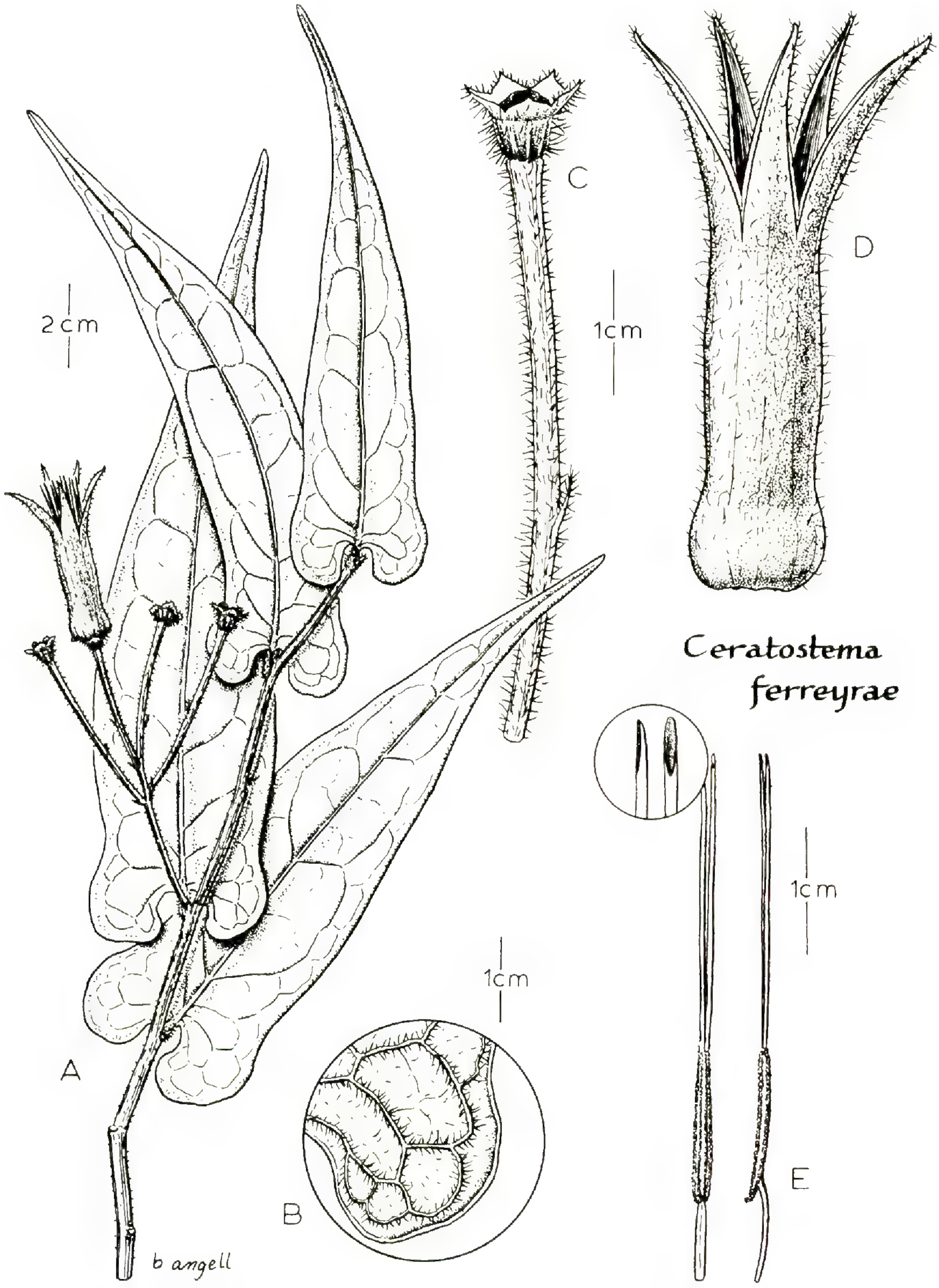

FIGURE 1. *Ceratostema ferreyrae* (from holotype): A, habit; B, close-up of leaf undersurface; C, calyx, pedicel, and bracteole; D, corolla; E, stamens, front and lateral views, with inset of dehiscence clefts.

purple when fresh; stamens 10, equal, ca. 40 mm long, the filaments distinct, ca. 6 mm long, the anthers ca. 35 mm long (including very slender tubules), with thecae 11–12 mm long, strongly papillose, dehiscence by subterminal, oblique clefts ca. 1 mm long; style equaling corolla, ca. 43–45 mm long. Fruits not seen.

TYPE. Peru, San Martín, Lamas, near tunnel between Tarapota and Yurimaguas, subtropical forest, 1100–1200 m alt., 2 Oct. 1973, *R. Ferreyra 18279* (holotype, NY, photo NY neg. 11115; isotype, USM).

Ceratostema ferreyrae is characterized by its narrowly ovate, long-acuminate, cordate-auriculate, amplexicaul leaves; costate hypanthium; inconspicuous calyx limb with short lobes; long corolla; minute floral bracts; and hirsute vestiture. It seems to be without close relatives, although its position in the key is probably indicative of general relationships. It is known only from the type collection.

Ceratostema ferreyrae is named in honor of Dr. Ramón Ferreyra, former director of the Herbario San Marcos (USM), who has been so helpful to itinerant botanists and has assisted me in many ways when I have been in Peru.

Ceratostema nodosum Luteyn, sp. nov. FIGURE 2A–C.

A C. megabracteato bracteis floralibus cuspidatis vel breviter acuminatis nec longe acuminatis, calycibus brevioribus (14 nec 28 mm longis), lobis brevioribus (2–2.5 nec 15–25 mm longis), sinibis late rotundatis nec acutis, corollis teretibus nec angulatis, basi cylindricis nec plus minusve gibbosis, secus lobos nec prope basem pilosis differt.

Terrestrial shrub 1–2.5 m tall; stems and twigs subterete, bluntly angled, densely white-pilose with unicellular hairs to 1.3 mm long. Leaves with petiole 2–5 mm long, terete, rugose, densely white-pilose; blade oblong, ovate, or elliptic, (4–)7–15 × (2.5–)3–7(–8) cm, coriaceous, the apex acute or short-acuminate, rarely obtuse or rounded, the base deeply cordate, auriculate with lobes well separated, amplexicaul, the margin entire, the upper surface short-pilose along veins proximally, the lower surface short-pilose throughout, the venation pinnate, with 3 or 4 lateral veins per side, these red when fresh, midrib and lateral veins impressed above and raised beneath, veinlets raised on both surfaces. Inflorescence solitary, axillary, racemose, ca. 15- to 20-flowered, nodding at anthesis but erect afterward; rachis 2–4(–5.5) cm long, subterete, bluntly angled, densely silky-pilose; floral bracts lanceolate to oblanceolate, 4–5 × 2–3.5 cm, membranaceous, the apex abruptly short-acuminate and somewhat mucronate, the venation prominent, the surfaces short-pilose, lower one pale green to rose-red when fresh, upper one rose-red; pedicels 10–12 mm long, 4 mm in diameter, subterete, densely silky-pilose; bracteoles located near or above middle of pedicel, lanceolate, 3–3.5 cm long, apically acute or short-acuminate, short-pilose on both surfaces. Calyx articulate with pedicel, 11–14 mm long, pale green when fresh, densely short-pilose; the hypanthium subcylindrical, ca. 6–7 mm long, 10-costate, the limb campanulate, ca. 5–7 mm

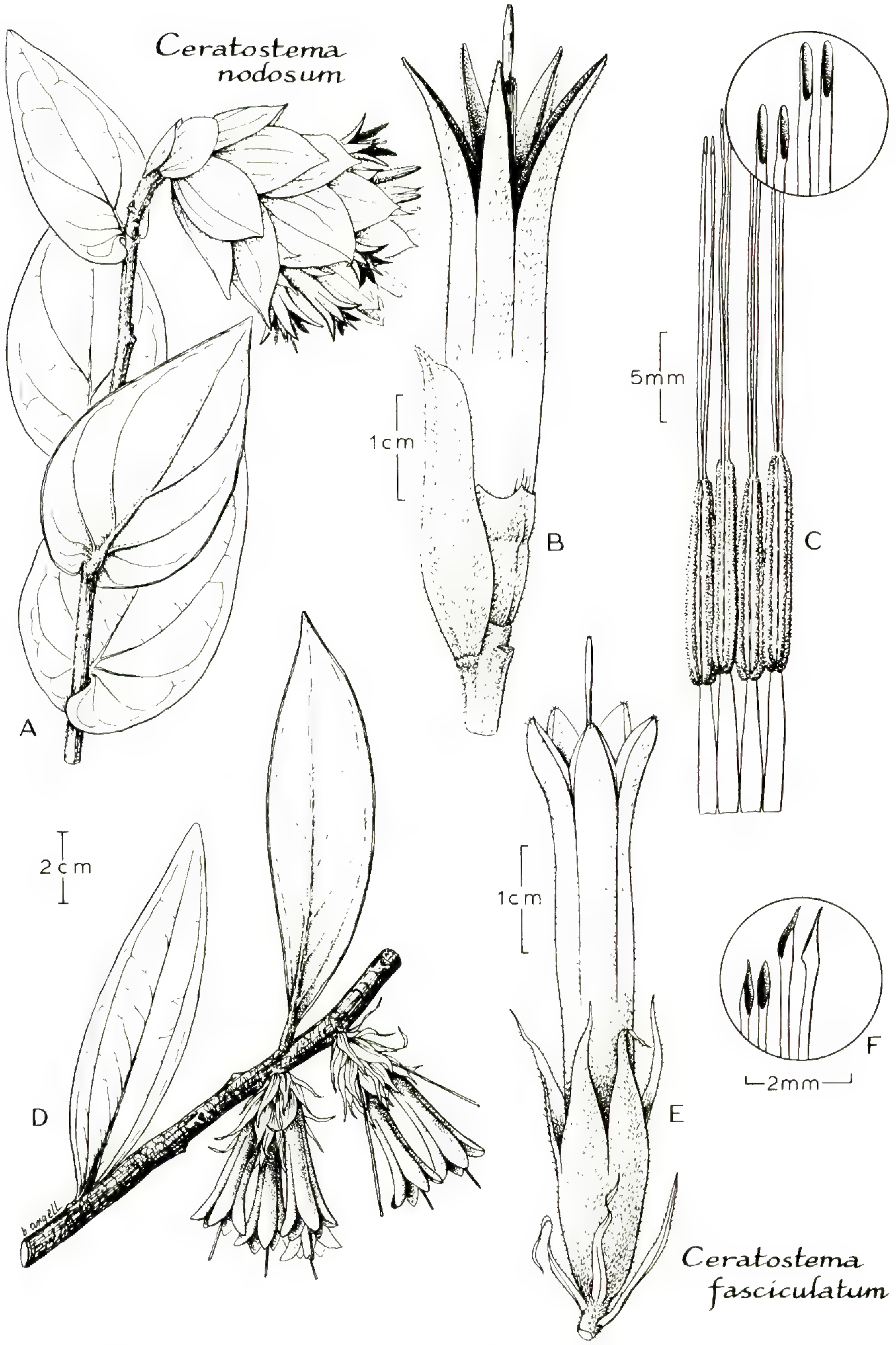

FIGURE 2. A–C, *Ceratostema nodosum* (from holotype): A, habit; B, flower, pedicel, and bracteole; C, stamens, front view, with inset of dehiscence clefts. D–F, *Ceratostema fasciculatum* (from holotype): D, habit; E, flower, pedicel, bracteoles, and floral bract; F, dehiscence clefts of stamens.

long including lobes, the lobes broadly triangular, acute, ca. 2–2.5 mm long, the sinuses broadly rounded; corolla cylindrical, terete, 41–45 mm long, ca. 8 mm in diameter, red when fresh, glabrous except short-pilose along lobes, the lobes narrowly triangular, long-acuminate, 12–13 mm long, dark purple within when fresh; stamens 10, alternately slightly unequal, ca. 39–40 mm long, the filaments distinct, ca. 9–10 mm long, glabrous, the anthers ca. 31–32 mm long (including slender tubules), with thecae 11–12 mm long, strongly papillose, dehiscence by subterminal, oblique clefts ca. 1 mm long; disc cupular, glabrous; style exserted, ca. 46–49 mm long. Fruits not seen.

TYPE. Ecuador, Napo-Pastaza, Baeza–Tena road, 25–28 km S of bridge in Cosanga, 1375–1460 m alt., 10 Jan. 1979, *J. L. Luteyn & M. Lebrón-Luteyn 6745* (holotype, NY; isotypes, AAU, CAS, E, GH, L, MO, P, QCA, US).

ADDITIONAL SPECIMENS EXAMINED. **Ecuador.** NAPO-PASTAZA: Salcedo-Napo, trail to Tena, 2390–2590 m, 7 Feb. 1977 (fl.), *Boeke 941* (AAU, NY, QCA); same location as type, *Luteyn & Lebrón-Luteyn 6739* (AAU, NY, QCA). TUNGURAHUA: Cordillera de Llanganates, valley of Río Sangarinas (Desaguadero), "La Trinca," 3000 m, 24 Nov. 1939 (fl.), *Asplund 9843* (L, S).

Ceratostema nodosum is characterized by its large, pilose, cordate-auriculate, amplexicaul leaves; relatively inconspicuous calyx limb and lobes; large, persistent floral bracts and bracteoles; and short pedicels. Superficially it resembles *C. megabracteatum* Luteyn, also from eastern Ecuador, in habit and coloration of flowers and bracts, but the differences are numerous (see diagnosis).

Ceratostema fasciculatum Luteyn, sp. nov. FIGURE 2D–F.

Ab aliis Ceratostematis speciebus hac notarum combinatione distinguitur: folia lanceolato-elliptica; bracteae ut bracteolae calycisque lobi anguste triangulares longe acuminati; corollae lobi pro rata breves.

Terrestrial shrub with branches to 0.75 m long; mature stems terete, brown when dry, glabrous; twigs complanate, bluntly angled, rugose, reddish brown when dry, densely short-pilose with unicellular hairs ca. 0.5 mm long. Leaves with petiole 5–8 mm long, terete, rugose, densely short-pilose; blade lance-elliptic, 9–13 × 3–5 cm, coriaceous, the apical portion acute although apex often blunt, the base cuneate, short-attenuate, the upper surface glabrous, the lower surface softly and densely short-pilose, the venation 3-plinerved from near base, midrib and lateral veins impressed above and raised beneath, veinlets impressed or slightly raised above and slightly raised beneath. Inflorescence solitary, axillary but often on older wood in axils of fallen leaves, fasciculate with 4 to 6 flowers; floral bracts narrowly ovate to nearly linear-lanceolate, long-acuminate, 20–25 mm long, ca. 3 mm broad at base, membranaceous, brownish when fresh, ciliate; pedicels ca. 6–12 mm long, subterete, striate, short-pilose; bracteoles located medially on pedicel, like floral bracts except 15–20 mm long. Calyx inconspicuously articulate with pedicel, 20–25 mm long, pale green when fresh, the hypanthium subcylindrical, ca. 3 mm long, terete, densely short-white-pilose, the limb cylindric-campanulate, 17–22 mm long including lobes, moderately short-pilose, the lobes narrowly triangular,

long-acuminate, 15–18 mm long, striate, the sinuses acute; corolla tubular, 38–43 mm long, bluntly angled, carnose, white at extreme base and between lobes but elsewhere bright red when fresh, sparsely puberulent, the lobes spreading, narrowly triangular, 4–7 mm long; stamens 10, alternately slightly unequal, ca. 40 mm long, the filaments distinct, ca. 9–10 mm long, white when fresh, the anthers ca. 33 mm long (including very narrow tubules), golden-orange when fresh, with thecae ca. 12 mm long, strongly papillose, dehiscence by subterminal, oblique, slightly flaring clefts ca. 0.75 mm long; disc cupular, glabrous; style long-exserted, ca. 50–53 mm long. Fruits not seen.

TYPE. Ecuador, Zamora/Chinchipe, Loja–Zamora road, km 29–31, ca. 2–4 km E of Sabanilla, 1700–1750 m alt., 1 Jan. 1979, *J. L. Luteyn, M. Lebrón-Luteyn, & B. McAlpin 6633* (holotype, NY; isotype, AAU).

Ceratostema fasciculatum is characterized by its lance-elliptic leaves; narrowly triangular, long-acuminate floral bracts, bracteoles, and calyx lobes; fasciculate inflorescences; and relatively short corolla lobes. It is known only from the type collection, found in a remnant patch of forest along a steep slope. The old, persistent inflorescences were infested with tiny ants. It seems to be without close relatives.

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